VOLUME LXIX NUMBER 6

THE
BOTANICAL GAZETTE

JUNE 1920

ECOLOGICAL SUCCESSION OF MOSSES

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 266

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(WITH TWO FIGURES)

The work on which the present study in moss succession is based has been confined, with the exception of that done at Mount Carroll, Illinois, to what may be termed the Chicago region. This includes localities showing the typical plant associations within about 40 miles of the city of Chicago. Since the deep rock canyon type of topography is entirely absent in this region, a study has been made of the Carroll Creek canyon, east and west of the town of Mount Carroll, which lies in nearly the same latitude as Chicago and about 125 miles west. The work was begun during the summer of 1916 and continued through the years of 1917 and 1918.

The nomenclature for the plant associations here employed is largely that used by COWLES (3) in his ecological work carried on about Chicago and other localities. Some of these terms may be traced back to WARMING (13), or perhaps farther. The first botanist to make use of this classification by which WARMING divided all plants into xerophytes, mesophytes, and hydrophytes in connection with bryophytes was WARNSTORF (14). Since that time EVANS and NICHOLS (5) have employed these terms in describing the mosses of Connecticut. The terms hydrarch and xerarch were employed by COOPER (2), and are here given the same meaning. The terminology for the classification of the moss species has

been confined wherever possible to that given by GROUT (7). The writer is under great obligation for the verification of all species and the entire classification of many to Mrs. ELIZABETH BRITTON, of the New York Botanical Gardens, Mr. GEORGE B. KAISER, curator of the Sullivant Moss Society, and Dr. LEROY ANDREWS, of Cornell University, and for many suggestions and other valuable assistance to Dr. HENRY C. COWLES and Dr. GEORGE D. FULLER, of the University of Chicago.

Description of region

The city of Chicago occupies a part of the land once covered by Lake Chicago (9). This was a post-glacial body of water formed in the depression between the Valparaiso moraine and the edge of the retreating ice sheet as it slowly moved northward. That the water remained comparatively stationary at certain levels for a considerable length of time after the recession first began, is proved by the presence of at least three distinctly defined old lake beaches. The Glenwood beach marks the edge of the Valparaiso moraine, and is the beach first formed by the impounded water; the Calumet beach was formed at a later period when the water was about 20 ft. lower than at the Glenwood stage; the third or Tolleston beach records a period when the water had receded until it was 20 ft. below that of the Calumet. The beach of the present lake is not far from 20 ft. lower than the level of the Tolleston stage of Lake Chicago, making the surface approximately 60 ft. below that of the original body of water. Going northward along the west shore of Lake Michigan one crosses, in the vicinity of Rogers Park, several old beach ridges of the Tolleston stage. Here the present lake is eroding material deposited by the older body of water. Farther north, about Winnetka and Glencoe, these old beaches have disappeared, and the lake is encroaching upon a bluff of morainic clay, where may be found all stages of clay ravines, from freshly eroded gullies to old ravines in an advanced stage of mesophytism. These ravines have their origin in the small streams which have cut back into the surrounding oak upland. Facing the lake the bluffs are in some places entirely bare of vegetation, while in others they have become well covered

with various species of trees and shrubs, such as *Thuja occidentalis*, *Juniperus communis*, and *Shepherdia canadensis*. On such stabilized bluffs, as well as in the mesophytic ravines, mosses form a conspicuous part of the ground flora. At other points north of Glencoe old dune formations are being eroded. The dune associations, however, are much better shown at the south end of the lake, so that no study of mosses on dune sand has been made along the west shore.

At the south end of Lake Michigan is an extensive sand dune formation reaching southward for some distance. The finer particles of the material eroded on the west shore are carried by the water currents toward the south and there washed up on the beach. The prevailing winds blowing from the lake catch up this fine sand as it becomes dry and carry it farther inland, thus continuing year after year the process of dune building (3). At almost any point which has been left undisturbed by man may be found all stages, from the bare foredune, through the series of cottonwood, pine, early oak, and the well established mixed oak dune formations. At Miller, Indiana, where a part of this work was carried on, the pine dunes are especially well illustrated to the south and east of the Grand Calumet River. This stream, which rises in eastern Indiana and flows almost directly west as the Little Calumet, makes an abrupt curve south of Calumet Lake. It formerly flowed eastward as the Grand Calumet, in a course nearly parallel with that of the Little Calumet, to its outlet into Lake Michigan north of Miller. Later, sand dunes began to form across the mouth, and the stream, being extremely sluggish, was not able to remove the accumulating deposit and was forced to find a new outlet, its present mouth near South Chicago, thus following the path of least resistance. The Grand Calumet now remains as a nearly stagnant body of water which is rapidly filling up with typical pond vegetation. The dune slopes south and east of this part of the river form one of the best moss habitats to be found in the dune complex. Much of the natural flora near the lake and along both banks of the river is being destroyed by the building of cottages. The level of the water in the Calumet has been raised by a dam recently built across the stream farther west. This has not only flooded the low

marshy land near the old outlet and many of the pine pannes north of the river west of Miller, but has submerged the lower part of a transition oak-pine slope south of the river where a special study of mosses had been begun in 1916–1917. Another similar, but perhaps somewhat more mesophytic, habitat is found near Tremont, Indiana, several miles east of Miller on a slope approximately at the same distance from the lake, and south of a smaller stream, Dune Creek, which also flows nearly west for some distance and here empties into Lake Michigan. This also shows a transition from the conifer to the deciduous type of trees, but contains some more mesophytic species, such as *Liriodendron Tulipifera* and *Acer saccharum*, not found at Miller. Mosses are even more abundant here than on the transition slope along the Calumet.

In addition to the region about Tremont and Miller the dune formations have been studied also at Paul, Pine, Long Lake, and Buffington, all located in Indiana. In all these places the same general conditions are met. Starting at the Lake Michigan beach and going southward may be found, in fairly regular order, first the foredune and cottonwood dune on which there is almost constant shifting of sand, followed by the slightly higher and more nearly established pine dune. This is often succeeded by a transition region of mixed oak and pine which merges into the oak dune proper, so that the oldest of the series and the one farthest from the lake is that of the established mixed oak dune on which *Quercus alba* and *Q. velutina* are dominant. These older dunes lie on the border line between the beech-maple climax region of the eastern United States and the oak-hickory climax which seems to be typical near the Mississippi River. For this reason it is somewhat difficult to determine whether these oak forests belong to the latter climax type, or are subclimax associations which will in time develop into the beech-maple type (3).

South of the dune complex just mentioned is another interesting type of topography very completely described by SHELFORD (10). This is a low swampy area made up of long shallow ponds or lagoons, nearly 100 in number, separated by ridges and extending almost parallel to the present lake shore. These ridges were formed by the building up of barrier beaches along the former

shore line, thus cutting off portions of the lake, which then became lagoons. At one time these ponds drained either into the Calumet River or directly into Lake Michigan. Much of this drainage has been cut off by railroad embankments built across the ridges and lagoons, so that these depressions now exhibit a characteristic pond flora. Some of the ponds have reached the shrub or swamp-forest stage; others are dominated by an almost pure stand of cat-tails or bulrushes; still others, ecologically younger, have a considerable area of open water. The ridges in most cases are covered with oak forests.

In addition to the lagoons, hydrophytic habitats are to be found in various swamps and bogs which lie within the Chicago region, all of which offer excellent conditions for bryophytic development. These may be divided into two main types, those which have developed from deep kettle lakes and those which have been formed from shallow lakes or ponds. The former type is illustrated by the bogs at Mineral Springs and Hillside, Indiana; while the latter is represented by the swamp forests at Thornton, Illinois, and Furnessville and Wilhelm, Indiana. The Mineral Springs bog has been developed by marginal encroachment of vegetation on the bottom and by formation of a surface mat in which *Decodon verticillatus* has played an important part. The progression has passed beyond the open water of floating vegetation stage, and even the early stages of mat formation seem to be somewhat telescoped; but here and there are small areas in which either the cat-tails, the bulrushes, or the sedges are dominant. This fen association merges into the shrub stage in which *Rhus vernix*, *Cephalanthus occidentalis*, and *Alnus incana* are most abundant. Beyond the shrub association is the tree area with *Larix laricina*, where in places the quaking condition is still quite evident. In the drier portions of the forest *Betula lutea*, a tree rare in the vicinity of Chicago, makes its appearance. The Hillside bog seems to have had the shrub stage, which here comes in on a dense growth of *Sphagnum*, continued until the substratum is comparatively dry, the forest stages having been subjected to a much greater retardation than is the case at Mineral Springs. The other swamps mentioned have been produced by marginal

growth of plant life on the bottom only. The Thornton swamp lies directly south of Chicago and between the Valparaiso moraine and the Calumet beach line. The Furnessville swamp is east of Mineral Springs, and at about the same distance from Lake Michigan. Both of these swamps have reached the forest stage of development, although there may be standing water in the depressions in the early part of the season. The third swamp, that at Wilhelm, is ecologically of a more advanced type. There is little standing water at any time, and the trees (oak, beech, and hard maple) indicate the approach of the climax forest.

Nearly all of the other associations under consideration are located on morainic drift, either within the region once occupied by Lake Chicago or on the moraine forming the uplands about its borders. Within the Chicago Lake area this till material has been somewhat worked over by water action, but not to a degree sufficient to entirely destroy its drift character. On the east bank of the Des Plaines River, just below its junction with the Sag, is the town of Lemont, Illinois. Here there is an outcrop of limestone which forms several small rock ravines. An abandoned stone quarry in the vicinity, as well as a stone wall at Palos Park and a quarry at Thornton, offer very similar pioneer rock surface habitats. East of Lemont near Palos Park on the edge of the Valparaiso moraine is an upland oak forest which is probably a subclimax forest. Excellent secondary successions in cut-over oak forest in various stages toward reforestation are found south of Lemont near Joliet. East of Joliet along Hickory Creek near New Lenox are much more mesophytic oak-hickory upland forests. At other places we find climax forests of the beech-maple type. At Smith, Indiana, a few miles east of the Wilhelm swamp forest, and at Otis, Indiana, southeast of Chicago, are primeval woodlands containing beech and hard maple of very large size, placing them without question in the climax area of the eastern United States. Along the Des Plaines River south of the northern boundary of Cook County, near Wheeling, Illinois, are mesophytic forests on uplands in which the presence of *Acer saccharum* indicates a greater degree of mesophytism than is frequently met with so far west in northern Illinois. No *Fagus grandifolia* has been

found in this region; but the maple may herald the coming of the climax forest of beech and maple. Directly east of Wheeling, along the lake shore at Glencoe, the upland forests are dominated by oak, although maple is present in the ravines.

The Carroll Creek canyon is a narrow valley with high and in many places nearly perpendicular walls of limestone. The stream meanders back and forth across the ravine and frequently washes against the rock wall. All successions, from the first pioneer lichens and liverworts to trees with decidedly mesophytic undergrowth, may be found within a short distance of each other. This is by far the best moss habitat which has been included in the present study. Although no evaporation data are available upon this region, it is probable that the excess of humidity over evaporation is greater than in the Chicago region proper; while the absence of dust from factories and smokestacks may also be a factor in favor of more luxuriant moss development.

Plant successions

All the successions studied may be placed in two general groups, xerarch successions and hydrarch successions.

Xerarch successions

Under the xerarch series are included all successions which have developed from or through xerophytic stages even though not xerophytic at the present time. Among the most important of these within the Chicago region are the successions on dune sand.

Sand dune succession.—The lake beach, while not strictly a dune formation, must necessarily be included in the dune series leading back from the lake. Here the sand is constantly being moved, either by the waves or, when dry, by the wind. Even during the summer the waves frequently wash over a space several rods in width; while in winter the effect of water and ice is felt still farther inland. Very few plants are able to gain a hold under such unfavorable conditions. Occasionally a few annual seed plants can be found; and sometimes upon the upper beach seedlings of the cottonwood and willows, as well as a few grasses, begin

a precarious existence. Mosses are entirely absent, no evidence having been found even of early germination stages. In addition to the continual change in the surface there is exposure to high evaporation, another factor very unfavorable to plant life.

The foredunes are a result of the obstruction offered to the sand laden winds by plants or other obstacles. Among the plants which may act as windbreaks are *Populus deltoides*, *Prunus pumila*, *Salix glaucophylla*, and *Salix syrticola;* or grasses, as *Ammophila arenaria* and *Calamovilfa longifolia*. There is no indication that mosses ever form a part of the flora. Exposure to evaporation and danger of smothering by sand are probably nearly or quite as great here as on the beach itself. As we enter the cottonwood dune, which is the first of the dune series characterized by trees, we still find constant shifting of sand. Evaporation, however, because of the shade cast by the trees, is somewhat less than in the earlier association. Gradually the sand increases in height about the trees, which continue to grow by adventitious roots (3). In time deposit of refuse from the cottonwoods and growth of ground flora add to the humus content as well as lead to stabilization of the sand. Occasionally under the larger trees or on the more protected leeward side of the dune a few mosses may win out in the competition and live. The first species to appear are such xerophytic forms as *Ceratodon purpureus*, *Bryum ventricosum*, and *B. caespiticium*. If well sheltered, these mosses may continue on into the *Pinus Banksiana* association; or if exposed by change in direction of wind, may be entirely killed out before the cottonwoods are replaced by pines. In no place on the cottonwood dune does there seem to be any considerable growth of mosses. The species mentioned form only scattered tufts or cushions, although in most cases sporophytes are borne freely. Either germination of spores does not often occur, or the young plants do not survive the unfavorable environment. These species probably do not spread so readily by vegetative growth as do many others.

From the cottonwood to the pine dune we usually find a gradual transition, in which *Pinus Banksiana* begins to appear more and more abundantly until the cottonwoods have been eliminated. At about this time *Pinus Strobus* becomes mixed

with *P. Banksiana* on the more mesophytic slopes, and eventually may form a pure stand. During even the early pine stages we may find a thick undergrowth of *Juniperus communis*, with or without *Arctostaphylos Uva-ursi*. These may last until the oaks begin to encroach upon the pines. Both the juniper and the pines produce a dense shade throughout the year, and by shedding needles form a layer of slowly decaying débris. Under the juniper, particularly on north facing slopes, we find the most abundant moss growth of the dune series. Beyond the juniper, where *Arctostaphylos* is very thick, mosses may be present but are less continuous. The bearberry is a plant of low trailing habit, and has the effect of shutting out the relatively small amount of light which penetrates through the dense covering of conifers, and renders photosynthesis on the part of the mosses difficult. The most abundant species of moss under the juniper is *Thuidium delicatulum*, ordinarily considered very mesophytic. Here it forms a thick continuous mat frequently excluding all seed plants as well as most other moss species, and extending beyond the juniper in many places. In this moss mat is a much smaller quantity of *T. recognitum*, not mixed with the *T. delicatulum* but growing in similar places and forming small but distinct portions of the mat. A still smaller amount of *T. abietinum* appears occasionally. Scattered through the *Thuidium* in very small quantities are two other mesophytic species, *Hylocomium triquetrum* found at Paul, and *Calliergon Schreberi* found at Miller. Both species are common in the mesophytic forests farther north (2). About 15 other species of mosses occur upon the pine dune. Some of these are found occasionally under the juniper, but more often on the sand in open places free from juniper, around the bases of trees, or on half-decayed sticks. The most common of these are *Ceratodon purpureus*, *Dicranum scoparium*, and *Funaria hygrometrica*, all of which are species of fairly varied habitat. Much the same condition has been found in all of the pine dunes studied. The mosses are most abundant in total quantity and are most luxuriant on north facing slopes, which in this region are also lakeward facing slopes. A greater number of species occur here than elsewhere in the dunes, unless it is in the transition oak-pine regions, where many

of these species continue on as relics while new ones make their appearance.

Just west of the pine dunes at Miller and south of the Grand Calumet is such a transition region of mixed pine and oak. Along the slope near the river is an abundant growth of mosses, but nowhere except close to the water do they form as complete a covering as in the pine association. Toward the top of the slope they become scattered, and there is also a decrease in the number of species. *Thuidium delicatulum* continues on the lower slope with some *T. recognitum*. Other types found among the conifers are mixed with new species, one of the most common of which is *Fissidens cristatus*. Other forms, either new or now much more abundant, are *Mnium cuspidatum*, *Thelia Lescurii*, *Anomodon rostratus*, *Climacium americanum*, and *Rhodobryum roseum*.

As mentioned previously, another ecologically more advanced transition slope occurs south of Dune Creek near Tremont, Indiana. Conditions here are even more favorable for mosses than at Miller. The presence of such trees as tulip and hard maple before the pines are entirely gone would indicate a telescoping of the oak stages and the rapid advance of the climax forest. The same relative difference in scattered moss patches on the upper slope and almost continuous mat near the base is noticeable here as at Miller. The most conspicuous species is *Aulacomnium heterostichum*, bearing numerous sporophytes. Other mesophytic species not mentioned before are *Bartramia pomiformis*, *Catharinea undulata*, and *Dicranella heteromalla*. *Anomodon attenuatus* occurs in dry situations, usually on tree bases. As already mentioned, both of these transition slopes are near the lake, north facing and south of streams. In striking contrast to these are transition slopes directly south of the pine dunes, farther from the lake, and not in close proximity to streams. Here we see a rapid thinning out of the moss flora. The more mesophytic species disappear entirely and only a few new forms come in. These resemble the types found at the xerophytic tops of the more mesophytic transition slopes.

In the early stages of the oak dune proper, either farther west along the Calumet or south of the pine dunes at Miller as well as at Paul and Furnessville, the mosses are still scattered. In

ravines, however, on slopes with a northern exposure or otherwise protected from desiccation, certain species may be fairly frequent. *Thelia Lescurii*, a gray-green moss growing in loose mats, is dominant and sometimes covers areas of several square feet. *Anomodon rostratus* also appears frequently, and *A. attenuatus* occasionally. *Climacium americanum* and *Rhodobryum roseum* may be found in sheltered spots but not in large quantities. *Ceratodon purpureus* is characteristic in open, less shaded places, while *Catharinea undulata* occurs here and there. A thick continuous moss carpet is never found among the oaks as in the pine

TABLE I

PRESENCE OF MOSS SPECIES IN ASSOCIATIONS OF SAND DUNE SUCCESSION

Species	Cottonwood	Pine	Transition pine-oak	Oak	Beech-maple
Anomodon rostratus	.....	P	P	P	.....
Bryum ventricosum	P	P	.....	.....	.....
Bryum caespiticium	P	P	.....	.....	.....
Catharinea undulata	.....	P	P	P	P
Ceratodon purpureus	P	P	P	P	.....
Climacium americanum	.....	P	P	P	.....
Fissidens cristatus	.....	P	P	P	.....
Funaria hygrometrica	.....	P	P	P	.....
Leucobryum glaucum	.....	P	P	P	.....
Mnium cuspidatum	.....	P	P	P	.....
Rhodobryum roseum	.....	.....	P	P	.....
Thuidium delicatulum	.....	P	P	P	.....
Thuidium recognitum	.....	P	P	P	.....
Thuidium abietinum	.....	P	P	.....	.....
Thelia Lescurii	.....	.....	P	P	.....

dune. As we go still farther south into the later stages of the oak associations, the moss flora becomes less, until about the only species left are *Thelia Lescurii* and *Catharinea undulata* in shaded places, with *Ceratodon purpureus* and rarely *Bryum argenteum* where the sand is more exposed. In forests where white oak is dominant and the forest floor is free from fallen trees, as is the case in many oak forests in this region, *Catharinea undulata* is usually the only moss species to survive. Table I shows the succession of mosses as they have been found in the xerarch series of the sand dunes. P indicates presence of species. Only the species which occur in two or more associations are included.

Why is it that we find this great variation in the moss flora within such a relatively small area as that included within this dune complex? There seem to be at least three causal factors which are worthy of special consideration. First is the constant transportation of sand; second, the exposure to high evaporation; third, and in this case of least importance, competition with other plants. Mosses, because of their low growing habits, are not able to endure covering. Even with such a genus as *Sphagnum*, which is able to continue upward growth year after year, and which has tall erect stems, it is not unlikely that a deposit of sand or sediment would entirely destroy its power of regeneration. There is much less probability that other species which do not have this advantageous habit could contend successfully against covering. Numerous places occur within this region where, through rejuvenation of some dune area, the sand is being carried over more or less mesophytic regions. North of the Grand Calumet near Miller are dunes which have reached the pine stage and which contain many of the species of moss found in the pine dunes south or east of the river. Recent changes, largely due to man, have brought about rejuvenation of the dunes to the windward. The mosses are now in many places early destroyed by smothering, because of the fine sand accumulating about them, and the whole slope, once mesophytic, is undergoing a retrograde succession. Thus it seems quite certain that any dynamic condition which will lead to covering will also bring about the death of any mosses already existing, as well as preventing the growth of the pioneer species. Contrary to the once common opinion, the soil of the new dune is not dry, except near the surface. The water table is always high, and it is necessary only to remove a thin layer of sand to find moisture, even during dry weather. The exposure to evaporation may be great, and this without doubt is the leading cause of the xerophytic structures to be found in dune plants, rather than non-availability of the water supply (**6**). The work of FULLER gives data upon evaporation in the dune associations, secured in this same region north of Miller. The results regarding the difference in the evaporation rate verify in a marked degree the conclusions to be drawn from the location of the xerophytic

and mesophytic types of moss. Stations for the location of the atmometers were selected in the cottonwood, pine, and oak associations near Miller, and for the beech-maple association at Otis, Indiana. The last, however, is upon morainal clay and not on dune sand. It is not necessary to enter into a detailed account of these results. Fig. 1, taken from FULLER'S work, shows the average of the mean daily evaporation rates in these associations for the three seasons 1910, 1911, and 1912. Fig. 2 indicates the curves for the average of the mean daily evaporation rates in the four associations for the growing seasons of these years.

The absence of mosses on the beach and the foredune is due to the continual change in the surface material and the exposure

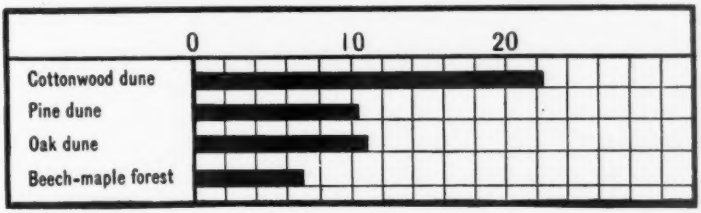

FIG. 1.—Average of mean daily evaporation rates for the 4 associations for seasons 1910, 1911, 1912.

to evaporation. Competition with other plants does not enter into the question. There is not the struggle with wave action on the foredune as on the beach, but there is still constant movement of sand by winds. The plants forming the nucleus of the foredune cast little shade, so that both desiccation by sun and wind and the probability of being covered by sand are as great as on the beach below. The cottonwood dune is higher, the trees afford much more shade, humus begins to accumulate, and as the dune tends toward stabilization there may be much greater protection from wind on the leeward side. However, even on a moderately windy day fine sand is deposited over the ground vegetation so that there is still the struggle to overcome the tendency to covering, and for opportunity for photosynthetic work on which the life of the mosses depends. Evaporation by exposure to bright sunlight and strong winds, while still high, may be somewhat less than on

the foredune. All of these causes tend to exclude any but the most hardy species, and even these are never abundant. The

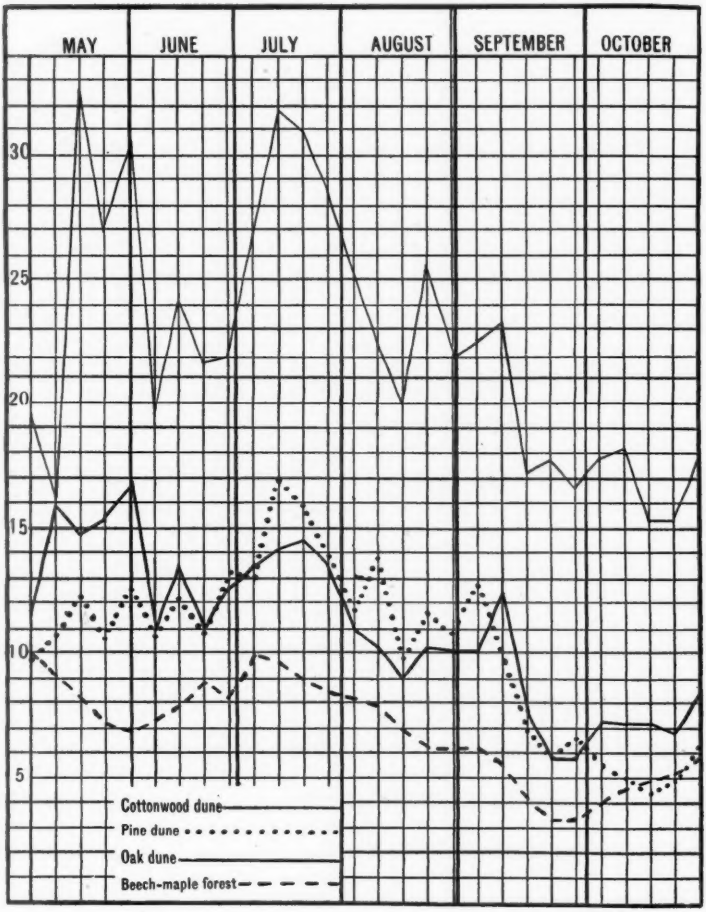

FIG. 2.—Average of mean daily evaporation rates in the 4 associations for growing seasons 1910, 1911, 1912.

struggle with other plants is not important, since there are always many unoccupied places, and the supply of available moisture is plentiful.

In the pine dune there is a much greater difference in the effect of the first two factors, moving sand and evaporation. It is here and in the mesophytic transition regions that the third factor enters into the causal conditions. According to the results of the evaporation work done by FULLER, the pine dune shows the lowest evaporation rate to be found among the tree associations of the dune series, other than the climax forest. It is still more significant that the rate is lower during the early summer and late fall, the most vital part of the season for mosses. The débris upon the ground aids in the absorption of moisture during rains. The moisture as it slowly escapes from the soil is confined near the surface by the close canopy of the juniper, and also by the dense overhead covering of pines. All of this leads to a high degree of humidity during spring and autumn, the seasons of greatest rainfall, not found elsewhere in the dune associations. In midsummer evaporation may surpass that of the oak dune (fig. 2), but the mosses by that time have passed their period of vegetative growth, and in many cases the production of sporophytes also. The maturing of sporophytes in other species, such as *Thuidium*, is carried on late in the season when humidity again rises. The fact that we find *T. delicatulum* as the dominant species under the juniper indicates decidedly mesophytic conditions, for except as a relic this species usually occurs only in moist habitats. Another reason for its dominance seems to be its ability to endure shade. Either there is no competition with other plants under the juniper or such plants have been crowded out, while *Thuidium* thrives best when well shaded. Other plants become competitive beyond the juniper where herbaceous vegetation, including several typically northern species, becomes more frequent. *Thuidium* less often covers extensive areas, and seed plants may even be found germinating on the mosses. In places more favored by light the mosses are likely to lose out altogether or be forced to take refuge on sticks or bases of trees. Another factor which seems worthy of consideration is that *Thuidium* grows directly on the slightly decayed needles of the conifers. These probably produce a chemical condition of the soil which effectively eliminates many other plants. While the pines also shed their needles, there is much

less material of this kind where the juniper is absent. The competition with shifting sand is nearly absent unless the dune is being rejuvenated. The deposit is so slight that it does not seem to retard either the germination of spores or spread by vegetative growth.

The two mesophytic transition regions from conifer to oak offer nearly as favorable moss habitats as do the pine slopes. Many of the species are relics from the more shaded former conditions, but which now are losing out, largely it would appear by encroachment of other light tolerant mosses, rather than because of competition with herbaceous plants. The shade is much less, especially during late fall and early spring. Many of the mosses are scarcely evident during midsummer. Most of them produce many sporophytes and mature the spores early in the year. That the relative humidity is at times increased by nearness to the water was quite evident on several trips to Miller when the weather previously had been warm enough to raise the temperature of the water of the Calumet. A strong cool wind from the north carried the mist, which was ascending from the river, directly over the transition slope. It was not learned how frequently this happens, but a considerable amount of moisture must be deposited during even a few hours of such a mist. This difference in humidity and water supply is probably one of the chief causes of variation in the luxuriance of the mosses on these slopes and on those farther from the lake, and not in the vicinity of other bodies of water. The evaporation rate at other times is very likely higher than on the pine dune, but unfortunately there are no data for evaporation on these transition slopes. Neither competition with other plants nor movement of sand is a very important factor, unless it may be the latter near the top of the slope.

On the oak dunes we again have an evaporation rate higher than that of the pine dune, except in midsummer. The sparse undergrowth in many places gives little protection from the hot sun which penetrates through the foliage of the oaks. During the spring and fall there is great exposure to somewhat desiccating winds. On many of the more mesophytic northward slopes where mosses might be expected there is often a dense growth of vernal herbaceous plants which seem to have crowded

out the mosses, until the latter are found only on decayed sticks or bases of trees. A few relics from the pine association occur here and there. On some slopes and in ravines where herbaceous forms have not taken full possession, mosses are more common. As previously mentioned, these are somewhat xerophytic species which appeared only rarely in the earlier succession, together with some relics from the former association. It is possible that the roots of the herbaceous plants, because of the need for moisture, rob the surface soil of its water and thus make it more difficult for mosses to secure a sufficient supply. Competition, therefore, can be said to be the great limiting factor on the more mesophytic slopes; while low humidity and high evaporation seem to be more important on those facing the south, where neither mosses nor herbaceous plants are very abundant. Sand laden winds are not of much importance unless the area is near a rejuvenating dune. In the older stages of the oak succession the forest becomes more mesophytic. There is less evaporation and higher humidity, with entire lack of covering by sand. Humus has now accumulated to a degree necessary for the growth of many more species of seed plants. Apparently these have become so successful as to cause almost total elimination of the mosses, which have contributed to their own extinction by adding to the humus content. Only in exposed paths or roads, on decaying logs, or sometimes on tree bases, do the mosses continue to exist at all. Old logs are rare in these woods, and only bases of old trees are favorable habitats, so that in the advanced oak association in this region the moss flora is often almost confined to a few species which spring up in paths or tracks left by the feet of animals.

We may summarize the causal factors for presence or absence of mosses in the dune succession as follows. Mosses are excluded from the flora of the beach and foredune by great exposure to desiccation and to covering by sand. Xerophytic species may appear on the cottonwood dune, but are prevented from becoming conspicuous by these same two factors. Mosses suddenly become abundant in the pine dunes, their growth being favored by high humidity and low evaporation during spring and fall, a result largely of the shade cast by the pines and juniper. Competition

with other plants begins, but is not of great importance; while that with shifting sand has nearly ceased. Whether the moss flora of the transition conifer-deciduous regions resembles more nearly that of the former or of the latter type seems to depend chiefly on local conditions, such as adjacent bodies of water and exposure to winds, greater humidity tending to increase the growth of mosses, and a high evaporation rate bringing about their destruction. In the oak dunes the higher evaporation leads to elimination of the relic species, while it may also lead to the appearance of new xerophytic types. Competition with other plants, especially vernal herbs, becomes a deciding factor, while that of moving sand may be omitted from consideration.

MORAINAL CLAY SUCCESSIONS.—The early stages of moss succession on morainic drift were studied near Glencoe, Illinois. On newly eroded bluffs along Lake Michigan mosses are absent, and in fact do not appear until after other vegetation has begun to take possession and the surface is no longer subject to very active erosion or slumping. On slopes partly covered with *Juniperus communis*, with or without *Thuja occidentalis*, mosses, while conspicuous, do not form a mat of large extent. The species are almost identical with those on sand at Miller. *Anomodon rostratus*, *Thelia Lescurii*, and *Thuidium delicatulum* are the most common. The same similarity on dune sand and morainic clay bluffs has been noted by COWLES (3) for the higher plants. Neither do mosses appear in the early stages of ravines while vertical erosion is active. In later stages, however, they become important and may take no inconsiderable part in stabilization of the surface. Unfortunately it was not possible to study ravines of all degrees of mesophytism, so that the exact period at which mosses appear was not determined. Most of the work was done in ravines having sides of rather gradual slope covered with a subclimax forest and mesophytic undergrowth. A vertical succession, not so evident on the dune slopes, is here a noticeable feature. In one such ravine *Polytrichum commune* is conspicuous among the arbor vitae at the top. Just below this is a good display of *Catharinea undulata*. About midway down the slope is a mixture of mesophytic species such as *Bartramia pomiformis*, *Dicranella heteromalla*, *Anomodon*

rostratus, and *Mnium cuspidatum;* while the lower third of the slope is nearly covered by one hypnaceous species, *Plagiothecium deplanatum*. The entire surface is well supplied with herbaceous undergrowth, but this has not yet been able to supersede the mosses, which, because of absence of decaying woody material, are found almost entirely on the ground. As the ravine widens and enters upon its second period of denudation, more light enters, and the mosses are gradually eliminated by their being a favorable habitat for the germination of seedlings of higher plants which can endure a greater degree of evaporation.

The oak uplands adjoining these ravines are characterized by an extremely impoverished moss flora with the exception of *Catharinea undulata*, which may occur frequently. This is almost equally true of the oak-hickory morainal forests at Joliet, New Lenox, and Palos Park. *Catharinea undulata* is present in all, *Physcomitrium turbinatum* occurs along paths, and at Palos Park *Leucobryum glaucum* is an occasional species. At Wheeling, Illinois, just west of Glencoe on the Des Plaines River, are upland morainal forests which are much more mesophytic than those just mentioned. Of these we may make two general divisions: those which have been pastured so that there are few shrubs and the herbaceous growth is almost confined to grasses, and those which have a mesophytic undergrowth both shrubby and herbaceous. In the unpastured woods, as a marked contrast with the other oak woods just mentioned, mesophytic mosses are common both on logs and on the ground. Among these are *Thuidium delicatulum*, *Mnium cuspidatum*, *Catharinea undulata*, and *Climacium americanum*. In the more open woods which have been partly cut over and subject to grazing, these same species continue on as relics, but are less abundant than before. With these may be *Leucobryum glaucum*, *Dicranum scoparium*, *Polytrichum commune*, and *Ceratodon purpureus*. It is not unusual to see rather large areas given over to *Leucobryum* and *Dicranum* alone or mixed with *Polytrichum*, *Catharinea*, and *Thuidium*. Close to the river, however, along the well drained bluff, we once more find only *Catharinea* on mounds and *Physcomitrium* with sometimes *Funaria hygrometrica* along paths and in tracks.

What is probably the ultimate forest of the region and the climax of the morainic series, the beech-maple type, is seen at Otis and Smith, Indiana. No mosses except *Catharinea* have been found in these forests in any place except on decayed wood or in water holes. In ravines in the Otis woods where humidity is higher (figs. 1, 2) mosses are a little more common, not growing on the ground, but on sticks, stumps, or bases of trees. These are almost invariably some species of Hypnaceae.

Of the three leading causal factors mentioned for the sand association, water erosion may be substituted for wind erosion and covering. As long as very active denudation continues on a lake bluff or ravine slope, resulting either in a gradual wearing down of the surface or in slumping, mosses have no chance to become established. While evaporation on the bare slope may be excessive, neither that nor competition with other plants is the primary factor. In the later stages, however, these become the two determining conditions. Wherever the arbor vitae and juniper are present we have a repetition of approximately the same conditions as under the pines and juniper on the dunes. The arbor vitae is near its southern limit at Glencoe and does not form a thick cover, and for this reason has less influence as a shade producer than has the pine. On the other hand, the juniper may be just as dense and as effective in producing shade and in retaining moisture as in the former situation.

ULRICH (12) has made a study similar to that by FULLER in the ravines at Glencoe. Three stations were used which correspond roughly to the three elevations on the ravine slope just described, and the results justify the supposition that evaporation is the main cause of such a difference. The station near the top in what would correspond to the *Polytrichum* area showed the highest rate of evaporation; that on the middle of the slope or the region of mixed mesophytic mosses gave a lower rate; that at the bottom or the area of Hypnaceae gave a still lower rate during a part of the season, although at times it was slightly in excess of that midway up the slope. This is exactly what we would expect from the nature of the species present and a comparison of the conditions in other regions where they are found. Competition with other

plants is no doubt an important factor on many such slopes, as they offer conditions increasingly favorable to other ground flora. Erosion decreases in importance as a determining factor in proportion as the mesophytism increases. When the ravine reaches its second denudation period, accompanied by greater sunlight and evaporation, the mesophytic mosses are eliminated along with the other mesophytic undergrowth; but these may reappear when the slope has once more attained a relatively permanent condition, and continue on until the climax association is reached, or may even persist into this association if logs and stumps are present.

In the open oak forests the moisture supply in air and soil probably is again largely the controlling condition, as in the oak forests on dune sand. Other plants do not occupy the ground to so great an extent as to exclude mosses because of lack of space alone, and there is little probability that the mosses would become shaded to a sufficient degree to shut out the light and prevent the necessary photosynthetic work. Just why there is so great a scarcity of mosses in the more mesophytic oak or oak-hickory forests, as well as in the beech-maple climax, both of which provide relatively high humidity and low evaporation rate (**6**), has not been fully determined. Competition with other plants may be accountable to a great extent, but even this does not seem sufficient to cause the almost complete elimination of mosses from these forests. In some places there is a continuous succession of dense ground vegetation during most of the growing season, which might be able to prevent the development of mosses; but in other places the vernal flora does not seem to be followed by a conspicuous aestival flora, yet mosses are not present. Perhaps the competition with the vernal flora in its prime, when most mosses attain their greatest growth, may be sufficient to prevent both spore germination and vegetative growth at this time, so that presence or absence of ground vegetation later in the year is of little consequence. The fact that when old logs are present, mosses are common upon them when not found on the ground, would indicate that they had not been able to hold their own against the herbaceous plants. Another factor which may have a

decided influence is that of the chemical change in the soil due to increase of humus. Just what the difference is which seems favorable to the germination of the seedlings of the climax trees and not to those of the former association, and how much of this difference is chemical and how much physical and related to light, are questions for future solution. Whatever it is, it would probably affect mosses as well as other plants. That an acid condition of the substratum alone is not detrimental is indicated by the luxuriant growth of many species on decaying wood and upon needles of conifers.

The great abundance of mosses in the upland oak forests along the Des Plaines River seems to be related to the slightly greater humidity of the atmosphere and larger supply of available soil moisture. There are indications that much of this region has been and still is at certain seasons somewhat swampy, so that there may be some question whether it belongs in the xerarch succession proper or should be placed in the hydrarch swamp series. While the final outcome would be the same in the two series, the intermediate successions would differ to a very large degree. The presence of the relic species in the grazed woods or partially cut-over land seems to be explainable by the fact that they are mosses of wide extremes of habitat, and are highly light tolerant. The change in environment appears to have taken place so gradually that the mosses have been able to become adapted to the greater xerophytism without themselves being materially altered.

The successions on morainic drift may be summed up in a few points. Mosses are entirely absent on the newly eroded bluffs and in the early stages of the ravines. They do not become conspicuous in the ravines until a rather advanced state of mesophytism has been reached, but they probably play an important part in the stabilization of the clay surface and addition of humus, which hasten the advance of the seed plants. Mosses appear in the conifer stage on the bluffs, forming part of the heath mat under the juniper. They are most abundant in the middle aged ravines, before the second xerophytic stage is initiated by the widening of the ravine and decrease of the angle of the slope.

On the oak upland and in most oak and oak-hickory forests of the subclimax type mosses are nearly absent, particularly where decayed logs are not to be found. The same paucity of mosses occurs in the beech-maple climax forests of this region, where competition with other plants or chemical conditions of the soil may be the leading cause. The increase in moss flora along the Des Plaines River at Wheeling seems to be a result of former and present better supply of moisture in soil and atmosphere.

Rock successions.—The rock successions are poorly represented in the Chicago region. The early pioneer stages of lichens and mosses, however, can be distinctly traced at Lemont, Illinois, near the Des Plaines River, on rocks of Niagara limestone which have recently been exposed, on the sides of an old stone quarry, on a cliff in an open pasture, and in several small ravines. The early crustose lichens are followed by *Bryum argenteum* and *Grimmia apocarpa*. *Ceratodon purpureus* seems to succeed these or even to appear with them on the flat rock surfaces, either on the top of the cliffs or on the bowlders. Many rocks have been exposed during recent excavations in straightening the channel of the stream. These are frequently well covered with crustose lichens, and the first moss to invade the lichen zone is *Bryum argenteum*, so that in this case at least this species is a pioneer moss. Elsewhere on rocks it seems often to come in later than *Grimmia*. At the mouth of the ravines, wherever the rocks are still exposed to xerophytic conditions, the struggle is going on between the mosses and lichens. The pioneer mosses usually smother out the crustose lichens, but in turn may be covered up by small species of the foliose lichen group. The mosses here never become very abundant, nor do they occupy large spaces. On the vertical faces there are numerous small cracks and pits in the rock which offer a better hold for typical crevice species, such as *Funaria hygrometrica* and *Gymnostomum rupestre*. Crevice forms are somewhat more abundant in the cracks of a stone wall at Palos Park where the mortar has disintegrated. At the quarry near Thornton, where the horizontal surface of the limestone has been denuded, there are numerous patches of *Funaria hygrometrica* and *Ceratodon purpureus*. Within the limits of Chicago, at Stony Island, although

the rocks have been long exposed, only very depauperate specimens of these same species occur. The later stages of the rock succession are absent. All of these places, with the exception of Stony Island, are surrounded by agricultural lands, and whatever has been the natural fate of this series has been too nearly obliterated by man to allow of its determination. At Stony Island the top of the rock is covered with prairie vegetation. The presence of a few oak trees seems to indicate that without the intervention of man the grasses would have been followed by an oak forest. The conditions at Lemont may have been much the same. In the ravines themselves the mosses belong almost without exception to the Hypnaceae and are without sporophytes, and hence are difficult to determine. *Brachythecium digastrum* is a rather common species.

The Carroll Creek ravine, where humidity is much greater and there is considerable seepage of moisture over the rock surface, is a much more favorable habitat for mosses than are the rock outcrops in the Chicago region. The number of species is not large, but those which do occur are plentiful and they form a thick covering over the rocks. Wherever the stream comes in contact with the rocks, and in other very moist places, liverworts are the first plants. Above the liverwort zone, or on rocks less closely in contact with the water, is the zone of crustose lichens. These are usually followed by foliose lichens, although quite often the pioneer mosses may succeed the crustose and contend for possession with the foliose lichens. The first moss is *Grimmia apocarpa*. On rocks in the open, exposed to strong insolation the greater part of the day, this species is abundant both on horizontal and vertical surfaces. Accompanying this is *Bryum argenteum*, which may occur almost if not quite as early, and in even greater quantity, particularly on horizontal surfaces.

This region offers the best illustration of a very definite succession of mosses on mosses. Here a second or even third moss stage is common and may occur on rocks in the open as well as on those in mesophytic shaded places in the ravine. The species which constitute the later stages differ in the two situations. In sunny places *Bryum argenteum* frequently forms the second stage,

with some Hypnaceae as the third vertical layer. An especially good example of this was found on a low rock situated on a hillside in an open pasture, and at some distance from the stream. The top of the rock sloped a little in the downhill direction and was slightly lower than the ground at the upper edge, but was perhaps 2 feet above the ground at the lower side. Numerous bushes overhung the upper border, but the lower part was exposed to full sunlight. On the shaded vertical face was a small quantity of a liverwort and an extensive growth of crustose lichens. The liverwort did not grow over the edge at the top, but the crustose lichens which had spread over much of the upper surface were being overgrown by foliose lichens. Growing among and over these was *Grimmia apocarpa*. Overlying the edge of the *Grimmia* and in many places entirely covering it was *Bryum argenteum*, forming a thick compact mat over a large part of the remainder of the rock, except at the upper side where soil had washed over the surface from the ground in contact with it above. Here *Brachythecium acuminatum*, growing partly on the soil, was extending out over the *Bryum*, forming a third moss layer. Small patches of lichens and of *Grimmia* here and there indicated that these at one time had been pioneer plants over the entire surface. When the two more mesophytic species came in, they had developed more rapidly on the part of the rock which received the most moisture from the ground and which was also somewhat shaded by overhanging bushes.

In shaded places along the creek in the ravine proper several species of *Anomodon* form the moss stage following the pioneers. As would be expected, the change in species occurs more rapidly in spite of the slope of the rock, which more nearly approaches the perpendicular. In some places the cliffs are quite closely covered with *Juniperus virginiana* and deciduous trees and shrubs. Under these and often overhanging the edge of the cliff is an undergrowth of *Taxus canadensis*, reminding one of the *Juniperus communis* under the pines in the dune region, except for the greater mesophytism which is indicated by the herbaceous flora. On vertical rock faces, well shaded and with water dripping over the surface, a luxuriant mass of *Anomodon viticulosus* is the only common

species. On surfaces with a more gentle slope, where the moisture supply is somewhat less but still plentiful, this species, either alone or with *Anomodqn rostratus*, forms the second moss stage. Where exposure to evaporation is greater, *Anomodon rostratus* alone, of the two species, occurs. Under the *Taxus* is a close moss carpet in which *Thuidium delicatulum* forms the third moss layer, and the second species is ordinarily *Anomodon rostratus*, which has smothered the *Grimmia* except at a very few points. Other species which help to make up this moss carpet often several inches thick are *Climacium americanum* and *Rhodobryum roseum*. This seems to be a moist habitat even during very dry periods. Another even better successional series was found on a rock on a more gradual slope, well shaded by deciduous trees of an older ecological association, and well above the level of the stream. This rock projected out a short distance from the bank, leaving a small space between the rock and the ground below. On this protected lower surface *Fissidens cristatus* formed a complete covering and in places extended up over the edge of the rock. Growing over this on the upper surface and reaching down over the edge at some points was a thick mat of *Anomodon rostratus*. Upon the *Anomodon* was a third stratum of *Thuidium delicatulum* and a small quantity of *Entodon cladorrhizans*, in all forming a compact mat of considerable depth. No traces remained of the typical pioneer mosses. The lichens showed occasionally under the *Fissidens*. On the *Anomodon* were patches of a powdery lichen and also of a fruticose species, showing that these may develop on the mesophytic mosses. *Climacium* and *Rhodobryum* again formed a small part of the last moss stage. Growing in this carpet of moss were such plants as *Pilea pumila*, *Geranium maculatum*, small ferns, and tree seedlings, indicating that the next succession is to be that of the vascular plants. Many such examples of the vertical succession of mosses are to be found throughout this ravine.

Such a moss carpet has been described by COOPER (2) for the rock surfaces on Isle Royale, and by BRAUN (1) for the conglomerate rocks near Cincinnati, Ohio.

At the top of the perpendicular cliffs there seems to be no special variation in mosses. Backward from the margin the same

pioneer xerophytic species soon give way to the more mesophytic ones. From the edge there is usually a rather abrupt slope upward for a few rods, which is thickly wooded, in most cases with oaks sparsely sprinkled with red cedar, and here and there a white pine. The undergrowth is decidedly mesophytic, and on the rocks are the same mosses already given for the other moist shady habitats. Immediately beyond the strip of wooded land are cultivated fields.

In comparing the sparse moss flora on rocks of the Chicago region with the very luxuriant display along Carroll Creek, where general climatic conditions must differ only slightly, one at once begins to search for the cause of the variation. While the rock exposures around Chicago are not extensive, they are sufficient to serve as a basis of comparison. The rock in both cases is dolomitic limestone, not differing enough in structure to be an important factor. The only outcrop which is near enough to Lake Michigan to be affected by the greater humidity is that of Stony Island, and that is, if anything, more barren than are the other regions. The cliffs and ravines at Lemont are not close to the stream as are those at Mount Carroll, but are on what was probably the river bluff at some past period when the stream contained much more water than at present, in all probability when the Des Plaines River was the outlet of the old Lake Chicago. Now the cliffs are not near any body of water, and in the ravines are only small streams which are nearly dry a part of the year. The stone quarry at Thornton is being worked by a cement factory, so that the exposure, with the exception of the rocks along the top, is too recent to afford any information. The amount of moisture which could come from the pool of water in the bottom of the quarry cannot be great enough to affect the flora on the horizontal rock surfaces above. The quarry at Lemont has been abandoned for some time, and much of the bottom is overgrown with weeds and grasses. The pools of water in the depressions may add slightly to the humidity of the air in the immediate vicinity; while the vegetation growing up from below and that overhanging from the upper edge of the rock undoubtedly adds to shade and contributes to a lower rate of evaporation. The

rocks near the Des Plaines River, thrown out in straightening the channel, have also been exposed for only a short time. It would seem therefore that the recent exposure in some cases and the distance from bodies of water sufficiently large to locally affect the humidity may be two of the reasons for the poor development of rupicole species. Another probably greater factor, at least for Stony Island and Thornton, is the large amount of dust which accumulates on vegetation, very effectually hindering photosynthetic work. At Stony Island there is much fine coal dust from smokestacks and trains, as well as dust from factories. At Thornton a large quantity of fine white dust thrown off from the cement factory accumulates in a thin layer and forms almost a crust, after light rains, on the foliage of all plants. There is less dust at Lemont, where there is a somewhat better development of mosses, but still much more than along Carroll Creek, which is bordered only by forests and farm lands, and is far from any factories. The later stages of succession on the rock outcropping near Chicago, as stated before, have been greatly interfered with by man. Evidently the change from pioneer conditions is extremely slow, and there is no development of true forest, so that all moss stages beyond the pioneer are so far wanting.

Returning once more to the Carroll Creek ravine, in great contrast to the Chicago region there is a narrow valley flanked by steep rock walls upon which direct sunlight falls for only a short number of hours each day. That this has much to do with the lower evaporation and higher humidity is indicated by the more mesophytic undergrowth and the greater luxuriance of mosses on all undisturbed north facing slopes. Whatever moisture enters the air through evaporation from the stream will be carried away slowly, since such a valley is well protected from winds. Another condition which also points to the moisture from the water as an important factor is that the greater growth of mesophytic mosses is found at places where the stream in its meanderings comes close to the rock wall, either on the north or south side of the ravine, and that the mosses are more luxuriant than in other places with a similar exposure but farther from the water. An additional cause may be found in the length of time in which snow

remains upon these north facing slopes. In places sheltered from the warm spring sunlight the snows melt slowly, and the moisture soaks into the humus instead of running off rapidly, as it must do on such an incline when the snow melts more quickly. It is well known that in general the moss flora becomes more conspicuous as we go north into the cold temperate regions. This condition is comparable to that of the northern habitats where much of the snow disappears under the action of sunlight and not of rains. Since these slopes are exposed to a lower degree of insolation even during the summer, the mosses are never subject to extreme desiccation. This cannot be true of the rock habitats which lie within the Chicago region.

The great economic importance of such a moss covering is demonstrated by the growth of seedlings of higher plants upon the moss mat, which leads to the initiation of the tree associations. Herbaceous plants grow to maturity and produce seed on moss covered rocks, with the roots obtaining nutriment only from the decayed moss material. The slower growing tree seedlings can exist in a like manner for several years, by which time their roots may be able to penetrate through the crevices or between the rocks to the soil below. Mosses are very hygroscopic and quickly absorb water during rains, but give it up slowly. Several days after rains water can be pressed from these mosses even though seepage is not an important factor. In addition to this is the immense value of a moss covering on rock slopes to conserve the water supply and prevent flooding of the adjacent land along the lower course of the streams. The great value of mosses in relation to the conservation of moisture and their effect upon the soil was observed by OLTMANNS (**8**). He says:

> A moss carpet acts as a sponge. A dense low carpet with countless capillary spaces between leaves and rhizoids absorbs capillary and superficial water, but obtains little or none by suction from soil and internal conduction. Consequently living and dead carpets of moss imbibe and evaporate approximately the same amount of water. A carpet of moss does not desiccate the soil . . . . they dry it to a less degree than does other vegetation, and they protect dry easily heated soil from desiccation.

EVANS and NICHOLS (**5**) also discuss the economic value of mosses in such situations.

The moss successions on rock surfaces may be summarized under two main heads: (1) There are at least four factors which are of special importance in accounting for the better moss development on rocks a long Carroll Creek than in the Chicago region: the greater humidity in the former place because of nearness to a stream and lessened exposure; a lower evaporation rate due largely to the fact that the rocks are sheltered from direct rays of the sun for a greater number of hours each day; the slow evaporation of the large quantity of water taken up by the moss mat during the gradual melting of the snow, and consequent lack of desiccation; and the freedom from atmospheric dust, common about any large city, which tends to retard photosynthesis. (2) Mosses are of special value on a rock substratum, as soil formers, to form a habitat for herbaceous plants, to initiate the early tree associations, to conserve water supply and to prevent floods by too rapid run-off, and to add to the aesthetic beauty of the landscape.

RIVER BLUFF SUCCESSION.—Another somewhat xerophytic habitat is that of a high river bluff as seen at Thornton, Illinois. In this region Thorn Creek, a comparatively small stream, has cut down much below its former level, resulting in drainage of the adjacent land and a consequent lowering of the water table. The trees along the bluff are deciduous and sufficiently scattered to allow penetration of the sun's rays, even during the summer. Because of grazing there is no shrubby undergrowth. Here are such mosses as *Catharinea undulata*, *Leucobryum glaucum*, *Ceratodon purpureus*, *Funaria hygrometrica*, *Polytrichum commune*, and *Physcomitrium turbinatum*, all of which are quite abundant. All of these, except the last, are found in the neighboring swamp forest. *Catharinea*, which is usually found only in the mesophytic forest, is probably a relic from a previous period of greater mesophytism. *Polytrichum*, while often found in rather dry places, seems usually to originate in mesophytic or even swampy habitats, so that it also is likely a relic. *Leucobryum* and *Funaria* have a wide range of habitat, and may be either relics from a more moist condition, or pioneers on soil constantly becoming more xerophytic at the surface. *Ceratodon* and *Physcomitrium* are doubtless sub-

sequent species, as they are found only in somewhat xerophytic species.

We have, therefore, a retrogressive succession indicated by the moss flora, which is a mixture of relic or antecedent, typically mesophytic species and the subsequent xerophytic forms. Such retrograde successions are not uncommon wherever surface conditions of soil water and exposure to evaporation have undergone rather gradual modification.

Hydrarch successions

Under this heading have been included all successions originating in water or very moist habitats, with the exception of the moist rock succession already described.

Floodplain succession.—This succession was studied at several points along the Des Plaines River, as at River Forest, Riverside, on the east bank at Wheeling, and also along Carroll Creek. The work has been of importance only for its negative value in establishing the fact of almost entire absence of mosses in such associations. Late in the season a few immature plants may sometimes be found, but these seem never to reach maturity if growing on soil, although a few well developed sporophytes may be found on plants growing on logs above the high water level. The true floodplain is subject to inundation during spring rains and during high water at any season. A great quantity of fine alluvial sediment is carried over the land and settles to the bottom with the recession of the water, leaving a crustlike layer of variable thickness over the ground and on any vegetation which may be present. The moisture conditions, except during the flood period, are favorable to spore germination; but the frequent deposit of fine material, particularly at the period when the moss plants would begin the season's growth, seems to be sufficient to destroy the ephemeral protonema which by any chance may begin to develop. The immature plants found later in the season probably come from late germination of spores which have escaped destruction or which have reached the floodplain from the surrounding uplands after the spring inundation.

Evaporation on a floodplain is not excessive, and the available supply of soil moisture is high, so that these two conditions

cannot cause the absence of mosses. Competition with the abundant herbaceous flora either in the spring or summer is only a secondary cause, if worthy of consideration at all. If competition were a prime factor, we should find somewhere in the floodplain succession, either in the horizontal series from the water back to the upland or in the series from the standpoint of time from the floodplain formed by the younger stream as it begins deposition, up to the old floodplain of the mature river which has nearly reached base level, an association in which mosses take an important part. This has not been observed on any of the floodplains under consideration. It is not, therefore, a case of being crowded out by other plants, but rather an inability to survive the unfavorable dynamic conditions along a depositing stream, which are as effective in eliminating mosses as was the active erosion of the earlier stages in the stream's development.

SPRING STREAM SUCCESSION.—At Otis, Indiana, and New Lenox, Illinois, are numerous springs, the water of which is highly impregnated with iron compounds. As the water comes in contact with the oxygen of the air, bog iron ore is produced which builds up mounds about the outlets of the springs until the water can no longer force its way to the top for escape, and finds a lower exit where there is less resistance to be overcome. Very frequently numerous species of plants make up a large part of the foundation structure of the tufa. Taking part in this tufa formation is a coarse moss, *Brachythecium rivulare*. The chemical substances in the water penetrate the plant tissues which, as they grow old, resist decay and form a porous rocklike mass. In the larger stream forming the outlet of such springs at New Lenox are several species of *Amblystegium* growing on submerged sticks and stones, but these do not enter into the tufa formation. A few other species, not typically water forms, grow on sticks which emerge from the water.

A somewhat comparable case of the formation of travertine in the waterfalls of the Arbuckle Mountains in Oklahoma has been described by EMIG (4), in which the two mosses *Didymodon tophaceus* and *Philonotis calcare* are the species involved. Still another species, *Cratoneuron filicinum*, has recently been collected by

COWLES at Turkey Run, Indiana, where it is a common species aiding in the tufa formation in the waters of similar mineral springs (11).

POND AND LAKE SUCCESSIONS.—The pond and lake successions may be classed in two general groups based on the ecological development. The early successions are represented in the Chicago region by two subdivisions, the pine pannes examined at Miller and the lagoons of Buffington and Long Lake, Indiana. The later successions may be found in the swamp forests at Wilhelm and Furnessville, Indiana, and Thornton, Illinois, and the bogs at Mineral Springs and Hillside, Indiana.

Early stages of pond succession.—Pine pannes.—The pine pannes are depressions among the dunes, so low that water which seeps through the sand from the lake, or in this case partly from the Grand Calumet River, reaches the surface or even may rise above it. Some of the depressions may be quite dry during the summer; others may have sufficient water to withstand ordinary summer drought, and remain wet throughout the year. Surrounding the more or less circular body of water in the center of the larger depressions is a border of pines of the same species as previously mentioned for the pine dunes. As a general rule we do not find a typical pond flora even in the center, probably because the quantity of water may be subject to great variation during the year. Sedges and marsh grasses are common, especially near the margin. Only one species of moss forms an extensive growth, namely, *Campylium stellatum*. It may be entirely submerged in the shallow water, but seems to thrive equally well along the edge where it emerges, and, as a relic from a former hydrophytic condition, may even be found on the higher ground at the edge of the tree zone. It is not a floating species in the pannes and is not found in deep water, yet it is the same species which forms much of the substratum of the floating islands in the lagoons at Buffington. While it cannot be considered as a tufa former, it aids materially in filling up such depressions. On the higher land among the trees other mosses are either absent or, if present, are of the same species as already given for the early pine dunes.

Lagoons.—The lagoons at Buffington have been described in the first part of this paper. The water is much deeper than in

the pannes, and the vegetation varies from the submerged species in deep water to the forests on the drier ridges. Floating in the deeper lagoons and sometimes emerging in the more shallow ones is a large quantity of *Drepanocladus fluitans*, *D. aduncus*, and *Campylium chrysophyllum*, and perhaps other closely related species. Around the margin of many lagoons are *C. stellatum*, already mentioned for the pine pannes at Miller, and *Bryum ventricosum*, which has also been found at Long Lake and Pine in much the same situations. In the larger lagoons are several floating islands, of which *C. stellatum* forms a large part of the foundation. In the larger lakes about Chicago, such as Wolf and Calumet lakes, the same marginal soil species of moss occur, but so far none has been found floating or submerged in the deeper water.

Wherever mosses appear, either floating or along the margin of ponds, they aid greatly in the conversion of depressions into land by promoting the advance of other terrestrial plants. There seems to be little difference in the mosses of the pannes and lagoons, except that which can be accounted for by the more shallow water in the former, which may subject the plants to seasonal periods of desiccation, and which would prohibit anything in the way of floating mosses or of floating islands. In both cases it is quite evident that mosses are an important class of plants in the early stages of the pond successions.

Late stages of pond or lake succession.—Swamp forests.—When comparatively shallow ponds and lakes pass from the aquatic conditions, the progress toward the later associations is by growth of vegetation upon the bottom along the margin. Waste material accumulates. In time the open water in the center is entirely eliminated, and a swamp results, which, depending on local conditions, may pass into a prairie where mosses take little part, or into a forest where they may be of prime importance. The Thornton and Furnessville swamps are illustrations of the latter type of development in rather early stages, while that at Wilhelm gives a later condition much more mesophytic. The first two are still characterized by depressions and hummocks, which are rarely encountered in the Wilhelm forest. Although humidity, shade,

and other factors of environment do not differ widely in the three areas, only five moss species have so far been found common to all. These are *Ceratodon purpureus*, *Mnium cuspidatum*, and *Catharinea undulata* on higher land or on logs, and *Brachythecium rutabulum* and *Amblystegium radicale* in low wet places. All except the first are mesophytic species. The *Ceratodon* occurs rarely and then on sticks which are in rather dry locations in the open or along the margin of the swamps. *Sphagnum* and *Leucobryum* are found only at Thornton, the former growing on the ground in depressions, and the latter on hummocks. Wilhelm far surpasses the other forests in the total quantity of the moss flora. *Thuidium delicatulum* grows abundantly on decaying logs and occasionally on the ground, and is perhaps the most conspicuous species with the exception of *Mnium cuspidatum*. *Thuidium recognitum* and *Anomodon rostratus* are found in smaller quantities, usually on logs or tree bases. Several of the very mesophytic species, such as *Climacium americanum* and *Rhodobryum roseum*, are common both on logs and on the ground. The shade is dense, and decaying plant material forms a thick layer on the forest floor. The moss display is of greater luxuriance than elsewhere in the Chicago region and is a close rival of that of the Carroll Creek ravine.

Bog forests.—The two bogs studied within the limits of the region under consideration are the tamarack bog of Mineral Springs and the *Sphagnum* bog near Hillside. Several typical associations in the ecological development can be distinguished: the sedge mat, shown at Mineral Springs; the shrub stage, well developed in both bogs; and the tamarack tree association at Mineral Springs. An additional division might be made of the *Sphagnum* moss association at Hillside, but this is a slightly different line of development rather than another ecological association.

As stated before, the bog successions are distinguished in origin from the pond successions, in that they are formed on sedge mats which grow out over the surface of deep lakes, forming quaking bogs, which may remain in a very unstable condition for many years. The first association to be found at Mineral Springs at the present time is a mixture of bulrushes, cat-tails, and

sedges, all of the early aquatic plants having disappeared. Mosses are about equally conspicuous over the whole of the sedge mat, and consist chiefly of six species, all long-stemmed and of somewhat upright habit of growth. They form a rather close packing about the roots of the other plants. All are very hygroscopic and grow partly submerged. The most noticeable is *Calliergon cordifolium*. The others are *Campylium stellatum*, *C. hispidulum*, *Drepanocladus aduncus*, *D. fluitans*, and *Brachythecium rivulare*.

In the shrub association, where the shade is somewhat increased, these species continue, but decrease in quantity. New species do not seem to come in until the late shrub or early tree associations which again show no distinct line of demarcation, but merge into each other. It is here that we get the first development of *Sphagnum* in the Mineral Springs bog. *S. palustre* occurs usually in low wet depressions and has not formed a very extensive growth either among the shrubs or in the tree association where it becomes more abundant.

COOPER (2), in his paper on the mosses of Isle Royale, discusses the presence and absence of *Sphagnum* in bogs. He concludes that *Sphagnum* comes in on the sedge mat following sedges of low growing habits, which produce little shade and offer only slight obstruction to the spread of the moss by vegetative growth. The inference is that *Sphagnum* does not germinate in shade, although it may spread into forests by vegetative growth from outside regions.

This theory does not hold for the swamps and bogs of the Chicago region. In the Mineral Springs bog the most common sedges are relatively large and coarse. At Hillside the early sedge stages are past, but the species still present are all tall and coarse. In the former bog *Sphagnum* does not appear on the sedge mat; in the latter *S. recurvum* has in most places entirely replaced all early associations. At Mineral Springs *S. palustre* begins in the transition shrub-tree area, and becomes most abundant among the tamaracks, where it is frequently found entirely disconnected with any present *Sphagnum* region even in the transition association. There is no evidence that it has spread from a less shaded place of germination on the sedge mat, and there seems to be no explanation of its presence other than that it has been able to

start under the shade of the trees and shrubs. North of the Mineral Springs bog is a low, flat, sandy plain covered with shrubs and marsh grass. The undergrowth is a compact mass of *Sphagnum*. In many old lagoons which have reached the shrub stage or which have a rank growth of swamp grasses, *Sphagnum* is growing in rather dense shade, but whether it originated in shade or sunlight cannot now be determined. Another case which is similar to that of Mineral Springs is the presence of *S. subsecundum* in isolated patches in the depressions of the Thornton swamp. There is no connection whatever with outside *Sphagnum* areas. In fact, no *Sphagnum* has thus far been discovered in the open regions around the swamp. Many of these patches are in the interior of the forest, and all are well shaded during the summer. It is quite true that in both the Mineral Springs bog and the Thornton swamp the trees are bare of foliage during the winter season, and therefore sunlight will reach the ground during the early spring. This argument, however, can be applied equally to the sedge association, where there is little shade from the coarse sedges until the new growth has begun. In this region, therefore, it appears that *Sphagnum* must be able to germinate under shade, and that it may be present in forests without having reached these habitats by vegetative encroachment from outside areas. This conclusion is borne out by work done upon the germination of *Sphagnum* by GEORGE L. BRYAN. The results of the study have not yet been published, and I am indebted to the kindness of W. J. G. LAND of the Botanical Department of the University of Chicago, under whose direction the work was carried on, for permission to refer to the results. BRYAN made many careful experiments upon the germination of *Sphagnum* spores under various conditions of soils and sunlight, and found that germination occurred in all degrees of sunlight and in darkness itself. Apparently there is some other determining factor which controls the presence of this group of mosses.

The tamaracks form a border about the bog. On the outer margin they are being displaced by other bog trees, as *Betula lutea* and *Nyssa sylvatica*. The tamaracks grow on hummocks, while the depressions between them may be very wet or even filled with

standing water. A large number of species of moss which have not been found in the previous bog associations occur here, on the ground, on sticks, or on logs. *Calliergon cordifolium*, the two species of *Campylium*, the *Brachythecium*, and *Drepanocladus aduncus* continue, often on partly submerged sticks. In slightly higher situations, but on ground that is still very wet, are *Leucobryum glaucum*, *Climacium americanum*, and *Thuidium delicatulum*. With the exception of *Leucobryum*, these species are also found on logs and sticks. *Anomodon rostratus* comes in where there is less moisture, particularly about tree bases. Here, as in the other mesophytic moss habitats, the soft hygroscopic mass of moss tissue forms a favorable place for the germination of tree seedlings and the seeds of other plants. As one approaches the higher land adjoining the sand dune to the north, the moss growth becomes less in quantity, but does not change very much in species until the dune itself is reached.

In the Hillside bog, a large part of which has reached the shrub stage, but in which there is much less water than at Mineral Springs, *Sphagnum recurvum* has been, and in places still is, the dominant vegetation. It must have reached a very luxuriant development in the recent past, but is now on the decline. In many places *Aulacomnium palustre* forms a second moss stage growing on *Sphagnum*, and this is frequently accompanied by *Polytrichum commune*. COOPER describes such an association in the *Sphagnum* bogs on Isle Royale. The bog itself has not yet developed the tree association, although with respect to moisture conditions it has advanced much beyond the bog at Mineral Springs. It is surrounded by climax beech-maple forest, and it is quite likely that this will be the fate of the bog if left to nature's influence. In the adjoining beech-maple forest *Catharinea undulata* is again the only moss of any prominence.

Table II represents the hydrarch succession from open water of lagoons and ponds to the climax forest. Once more the great importance of pioneer mosses in the advancement of the higher plant associations is shown. The economic value of shallow ponds is slight; while on the other hand they may be very injurious in that they harbor larvae of insects, harmful to man, so that the

elimination of such swampy regions may be very desirable. By the filling up of depressions the area may be made productive either as prairie or forest. The poorly drained deeper ponds are probably as little to be desired from an economic standpoint, since the water will not support the life of aquatic animals of commercial value. Consequently any natural agency which will further the change from hydrophytic to mesophytic conditions will add to the number of acres of productive land reclaimed from a state of total non-productivity, and also lead to better health conditions for the inhabitants of the surrounding country.

TABLE II

PRESENCE OF MOSS SPECIES IN ASSOCIATIONS OF HYDRARCH SUCCESSION

Species	Open water	Sedge mat	Tamaracks	Swamp forest	Beech-maple
Amblystegium riparium	P	.....	P	.....	.....
Anomodon rostratus	.....	.....	P	P	.....
Aulacomnium palustre	.....	P	.....	P	.....
Brachythecium sirulare	.....	P	P	P	.....
Campylium stellatum	P	P	P	.....	.....
Campylium hispidulum	.....	P	P	.....	.....
Calliergon cordifolium	.....	P	P	P	.....
Climacium americanum	.....	.....	P	P	.....
Catharinea undulata	.....	.....	.....	P	P
Drepanocladus aduncus	P	P	P	.....	.....
Drepanocladus fluitans	P	P	.....	.....	.....
Dicranum scoparium	.....	.....	P	P	.....
Entodon cladorrhizans	.....	.....	P	P	.....
Leucobryum glaucum	.....	.....	P	P	.....
Mnium cuspidatum	.....	.....	P	P	.....
Polytrichum commune	.....	.....	P	P	.....
Rhodobryum roseum	.....	.....	P	P	.....
Stereodon haldanianum	.....	.....	P	P	.....
Thuidium delicatulum	.....	.....	P	P	.....
Thuidium recognitum	.....	.....	P	P	.....

The pannes about Miller are mostly of recent origin and are not within easy reach of other habitats of aquatic mosses. This may account for the fact that the few species are present. The mosses found growing in all of these ponds, so far as observed, propagate vegetatively only, or with very rare spore production, thus virtually prohibiting their spread into distant ponds except when carried by birds or other animals. As previously mentioned, these mosses must be able to make a good recovery after periods of desiccation, and must also be able to resist covering to some extent, as these pannes

are subject to occasional dry seasons and frequent deposit of sand. The presence of the mosses soon leads to accumulation of humus over the sandy bottom and initiates the growth of semihydrophytes.

In the lagoon region is a far more extensive pond area, both as to actual number of ponds and variation in ecological development, caused by depth and size as well as by age of the individual lagoons. The chance for transfer of mosses from one pond to another is much better; the variation in depth permits the growth both of floating and fixed species, while the greater age has allowed time for accumulation of more humus, which leads to the introduction of still other species, as well as perhaps a more luxuriant growth of all. With these conditions comes the rapid advance of the shrub and forest or prairie successions. In the swamp forest the moss flora becomes increasingly a dominant factor in humus accumulation as the ecological succession advances toward the climax, but begins to decline with the close approach of the beech-maple association. This appears to be a result both of competition with other ground flora and of the smaller supply of available water near the surface.

Very little work has been done in determining conditions for plant life in the bogs, but from the xerophytic structures of many bog plants, and the shallow root systems of the trees, COWLES concludes that, while moisture is plentiful, the chemical content of the water is such as to have a toxic effect upon the root development of plants, and to prevent absorption of water to a great extent. In other words, this is a physiologically xerophytic habitat for seed plants. It is not known how far this may influence the development of mosses; that it is not very injurious is proved by the great abundance of some species, such as *Sphagnum*. On the sedge mat the shade may be considerable when cat-tails are abundant, but the sun's rays reach the ground more directly than in the forest. The humidity near the ground is probably greater than among the trees, but evaporation at times is also much greater. The mosses occupy the small spaces around the roots of the fen plants and often cling closely to them, forming a packing between the stems, but there are no large masses. In some places there is a luxuriant growth of marsh forget-me-not and other species of

low growing seed plants which nearly smother out the mosses. The increase in shade and possibly other conditions in the late shrub stage and early tree association apparently are unfavorable for most of the old herbaceous species, and new ones have not taken their places, so that there are large areas unoccupied by such ground vegetation. As in the pine dune, so also here we may have toxicity produced by decay of conifer needles. This probably does not greatly retard the moss development, although it may account in part for the change in species. With herbaceous plants, on the other hand, it may result in almost total elimination. The rapid increase of quantity and number of species of moss in the early tree association, therefore, is directly related to these environmental conditions. The greater shade and lower temperature are both more favorable to moss growth, and added to these is the lack of competition with other plants.

As the tamaracks are replaced by deciduous trees, the mosses give place to herbaceous seed plants. The chemical condition of the subsoil changes, more humus accumulates, moisture and humidity decrease. The mosses now are crowded out of their former locations until, with few exceptions, they persist only on sticks, logs, and tree bases, and we find in their place many ferns and seed plants. Competition seems to be the great cause of the elimination. Some general conclusions regarding the pond and lake successions of mosses are as follows.

Very few mosses appear in the pannes, but those which are present are coarse and aid in filling up the depressions. The lagoons are favorable habitats for floating species, while other mosses are abundant along the margin. Both produce material which is added to the muck on the bottom and which provides nourishment for other plants. Still other species assist in the formation of floating islands. In the bogs a few species of semi-aquatic mosses appear in the early fen stage in considerable quantities. There is a slight decrease in quantity in the shrub stage. A marked increase in quantity and number of species is evident in the early tamarack association and continues until the tamaracks are replaced by deciduous trees, making the tamarack the dominant moss association. In the later deciduous association there is

a continuous decline in the moss flora until the climax beech-maple forest is reached. Competition with other plants seems to be the determining factor as the successions advance beyond the semi-hydrophytic.

Conclusions

1. In the successions on sand, mosses are most abundant, both in number of species and in total quantity in the stage; in which they first become very noticeable, the pine stage; and they decrease through the early oak stages to either the oak or the beech-maple climax.

2. In the swamp and bog successions the greatest dominance of mosses is found usually in the swamp or bog forest association, which may or may not directly precede the climax.

3. The mosses found in running spring water and in stagnant water are of different species, but nearly all belong to the same family, the Hypnaceae.

4. The succession on floodplains is unimportant because of constant deposit of sediment over the germinating mosses.

5. Mosses are among the highly important pioneer plants on bare rock surfaces, and continue abundant far into the forest association.

6. From an economic standpoint mosses are of the greatest value in several respects. They are soil formers and provide favorable habitats for germination of higher plants. They assist largely in forming the surface mat over deep lakes and in filling up shallow bodies of water. They may take part in building up rocklike substances, as tufa. They help to make up floating islands on which higher plants may grow. They conserve moisture, and give it up slowly, thus aiding in the prevention of disastrous floods in the surrounding regions. They prevent erosion of clay or sand surfaces.

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OVULIFEROUS STRUCTURES OF TAXUS CANADENSIS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 267

A. W. DUPLER

(WITH PLATE XXIII AND SIXTY FIGURES)

Introduction

Following a recent paper (13) in which the writer gave a description of the staminate structures of *Taxus canadensis* Marsh., this paper deals with the ovuliferous structures, namely, the primary shoot, the secondary shoot, and the ovule, describing both the development and vascular features, together with a discussion of the morphological questions raised by these structures. The purpose in this investigation was twofold: (1) to compare *T. canadensis* with the European *T. baccata*, and (2) to look for new evidence bearing on the morphological problems of these structures in the genus. While no pretense of finality is made in this connection, it is thought that some additional evidence has been secured bearing on these problems. Since the female gametophyte has already been described (12), only such reference is made to it as may be necessary. For a statement as to materials and methods, the reader is referred to previous papers (12, 13).

Historical

Taxus has engaged the interest of botanists for a long time, the ovulate features, the gametophytes, and the early embryogeny especially receiving attention. The literature dealing with the ovulate structures is quite extensive, much of it being found in connection with descriptions and discussions of other conifers, and is based almost entirely upon *T. baccata*, very little dealing specifically with *T. canadensis*. The two forms are similar (6), and much which has been written will apply equally well to both forms. It would be impracticable to include a complete summary of all that has been published on the subject, a general summary sufficing,

more complete references being available in the accounts of STRASBURGER (35), RADAIS (24), and WORSDELL (39).

The earlier work was based largely on external features, and attempted to homologize the structures with those of the angiosperm flower. This attempt seemingly persisted much later with *Taxus* than with most other conifers, the gymnospermy of *Taxus* not being quite so soon recognized as in other forms. The bulk of the literature deals with the more theoretical questions, the actual descriptive work not being so extensive. The discussion of the literature will be presented in the text of the paper, in connection with the several topics, in this way avoiding repetition and presenting each topic in more complete form.

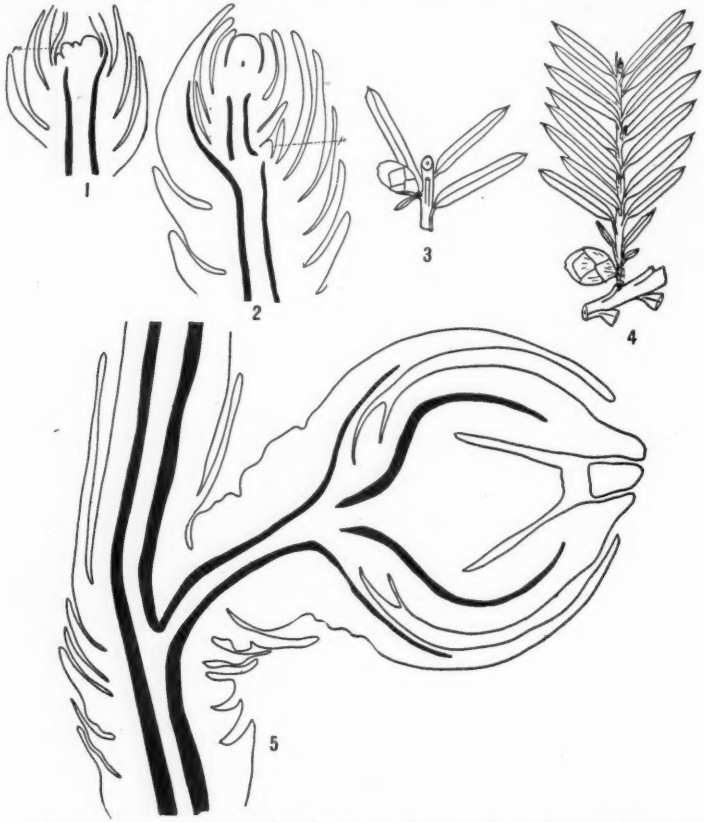
Ovuliferous bud

As previously pointed out (13), three types of buds are formed in the axils of the leaves of a current season's shoot, namely, vegetative, staminate, and ovuliferous. The differentiation of the last is first recognized by the appearance of the rudiment of a secondary axis in the axil of one of its uppermost scales (fig. 1), this rudiment appearing early in July. The ovuliferous bud begins early in the spring, as a conical rudiment in the axil of a young leaf, shortly after the beginning of the growth of the vegetative shoot, forming usually nearer the tip than the staminate buds. STRASBURGER (36) found the first differentiation of the ovuliferous bud in *T. baccata* to occur about August 1. The structure can be distinguished by external features with certainty only when the ovule has reached such size as to protrude beyond the scales, usually not until spring. JÄGER (15) says that the ovuliferous bud of *T. baccata* is evident about February 1, being slightly yellowish, and the vegetative bud being reddish brown; but this is hardly a safe criterion, owing to color variations.

Primary shoot

GENERAL FEATURES.—The ovuliferous organ in *Taxus* consists of two structures: the primary ovuliferous branch, or, as it is more generally known, the primary shoot; and the secondary shoot on which the ovule is borne. The primary shoot arises directly

in the axil of the leaf, and, as STRASBURGER (35) pointed out for *T. baccata*, begins with two transverse scales, following which are a number of scales in spiral order, in the axil of one (or two) of



FIGS. 1–5.—Fig. 1, long section of primary shoot showing rudiment of secondary shoot; fig. 2, secondary shoot with young ovule and primary axis tip pushed to side; fig. 3, primary shoot which has developed two small leaves, shown below ovule; fig. 4, primary shoot which has become functionally vegetative, showing ovule at base; fig. 5, median longitudinal section of primary shoot, secondary shoot, and ovule, such as fig. 4; figs. 1, 2, ×24; fig. 5, ×17.

which the secondary shoot (or shoots) arise. The scales of the primary shoot are very similar to the scales of the staminate

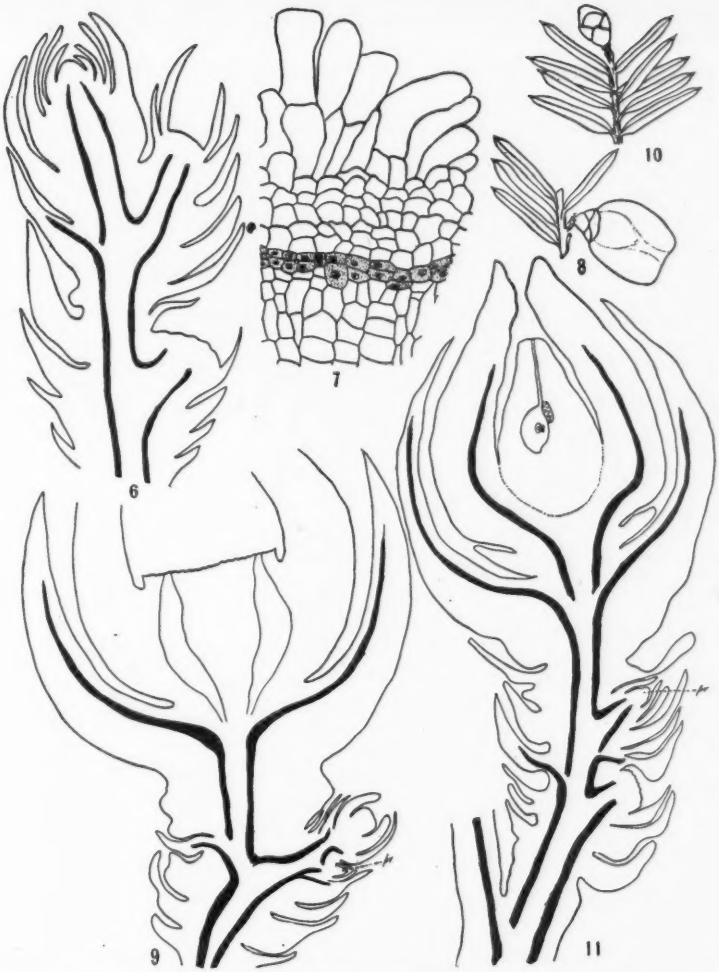
strobilus already described (**13**), having very thick epidermal walls, especially on the outer surface, stomata on the inner surface, and rather large air spaces. They are brownish and lack chlorophyll.

During its first season the primary shoot is a dwarf branch of limited growth, and the development of the secondary shoot results in its tip becoming pushed aside (fig. 2) and remaining dormant for a time. Externally this gives the appearance of a single structure with a terminal ovule, a situation which may explain some of the earlier views as to the position of the ovule. VAN TIEGHEM (**37**) apparently was the first to point out this behavior of the primary axis. According to SCHUMANN (**31**), and also PILGER (**23**), the primary axis ends blindly, and the so-called tip of the primary shoot is the knob of a reduced side shoot which may at times grow out to form a second secondary shoot. When this occurs the primary axis may form a short knob between the two secondary shoots. This view does not agree with the facts and has received but little support.

SECOND SEASON'S GROWTH.—The tip of the primary shoot remains dormant until the next spring, when its growth is renewed, resulting either in its continuation as a dwarf structure, as in the first season, or in its growth as a leafy shoot, like that from the ordinary vegetative bud, a fact first noted for *T. baccata* by STRASBURGER (**35**). This leafy shoot may bear only a few small leaves (fig. 3) and develop no further during the second season, the subsequent behavior of such small shoots not being known. It also may develop as an ordinary leafy branch, differing in no way from other leafy branches except in bearing the secondary shoot at its base (figs. 4, 5), and, like any other vegetative branch, bearing vegetative and reproductive buds of the next season. Occasionally the primary axis remains dormant as a vegetative bud for a season or more. In such cases the reproductive nature of the first season can be told only by the scars of the old secondary shoot (fig. 6). Normally, however, the primary shoot continues its dwarf and reproductive character for the second and later seasons, producing a few scales as in the preceding season, with one or two new secondary shoots on the new growth. It has been generally assumed that the primary shoot produces fruiting structures for only one

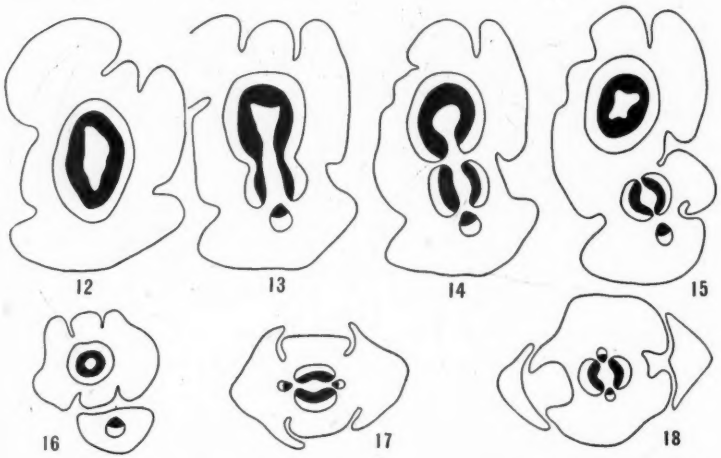
season, and that the maturity of the secondary shoot with the ovule results in the death of the primary shoot as well. This is not the normal situation, as usually only the secondary shoot with the ovule drops from the primary shoot, which remains in the axil of the leaf, a branch scar showing the place of detachment at the secondary shoot from the primary shoot (fig. 6). Detachment of the secondary shoot is probably accomplished normally by the formation of an absciss layer across the base of the shoot. The region of abscission is marked by a narrow layer of platelike cells, rich in protoplasm, outside of which is a layer (5–6 cells wide) of cork tissue, and whose outer border consists of radially elongated cells which form a conical cap to the scar (fig. 7). When collections of *T. canadensis* for this study were first begun, in the autumn of 1913, it was noticed that ovulate buds were to be found on older as well as on the current season's growth, as has since been pointed out for *T. baccata* by Miss AASE (1). This is not due to dormancy of buds which had failed in development, as might usually be assumed, but to the persistence of the primary shoot year after year, producing one or two new secondary shoots each season. This renewal of growth is contemporaneous with that of the primary shoots of new branches, beginning early in the spring, although not becoming recognizable externally until later in the summer, when it can be distinguished by the slight projection which appears at the base of the secondary shoot (fig. 8). Growth is slow, and by the middle of July is arrested, as in previous seasons, by the growth of the new secondary shoot (fig. 9). As these observations show, the primary shoot is a persistent structure and may produce secondary shoots season after season, or become a leafy shoot, the situation being evidence against regarding the primary shoot with its secondary shoot as representing a compound strobilus.

TERMINAL PRIMARY SHOOT.—Several cases were found in which the primary shoot was a terminal structure of the leafy branch (figs. 10, 11), the terminal bud having developed as a primary ovuliferous structure, bearing a secondary shoot. That this may continue to function as a primary shoot for more than one season is shown by the presence of a secondary branch scar a little



FIGS. 6–11.—Fig. 6, long section of primary shoot showing scars of secondary shoots of two previous seasons; primary axis remaining dormant, not producing secondary shoot the season collected; ×24; fig. 7, detail section through scar (note shaded abscission layer and corklike wound tissue external to it); ×140; fig. 8, primary shoot with mature ovule and projection at base of ovule showing external appearance of a normal second season's growth of primary shoot; fig. 9, longitudinal section of primary shoot showing half-grown ovule of current season and young ovule of next season (primary axis tip shown below younger ovule); ×17; fig. 10, terminal primary shoot; fig. 11, longitudinal section of terminal primary shoot (leaf base shown at lower end of figure; note branch scar, left by secondary shoot of preceding season, and that primary axis tip has begun growth for third successive season); aril shown at base of ovule; ×17.

distance below the tip of the primary axis (fig. 11), in which the tip of the primary axis has also begun its renewal of growth for the third successive season. No case was found in which it was known that a terminal primary shoot later became functionally vegetative; but in view of the occasional behavior of the primary shoot as a leafy shoot, it is very possible that a terminal primary shoot may again become vegetative in function.

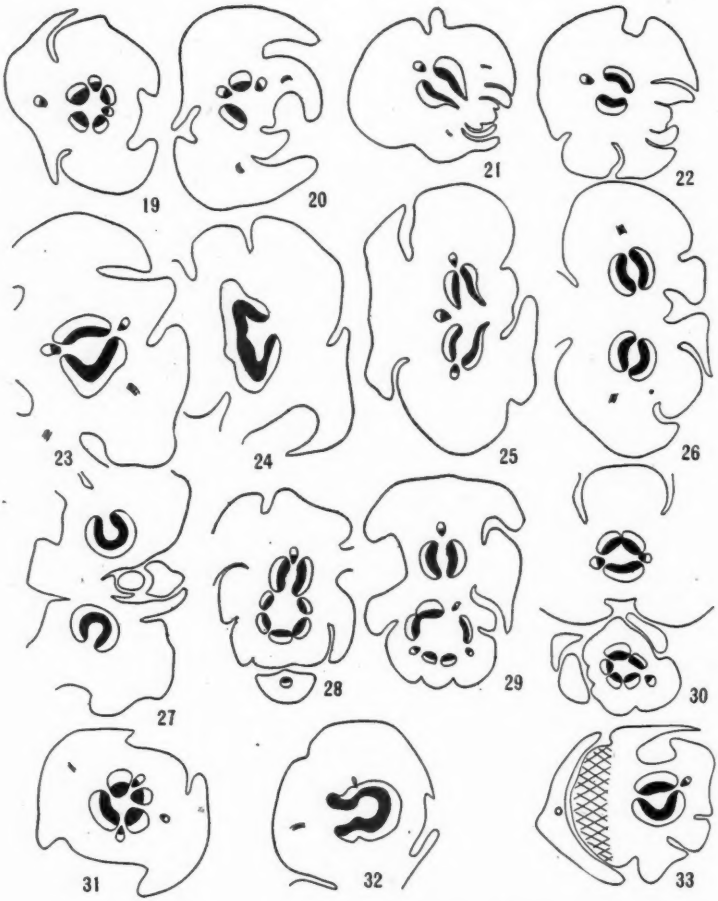


FIGS. 12–18.—Series at different levels showing vascular supply from leafy shoot to primary shoot: fig. 12, vascular cylinder of leafy shoot; fig. 13, trace to fertile leaf and formation of vascular strands to primary shoot; fig. 14, vascular strands for primary shoot separated from main cylinder, showing branch gap; fig. 15, main axis cylinder closed with primary axis cylinder and bundle of fertile leaf farther removed; fig. 16, primary axis cylinder closed; figs. 17, 18, bundles to lower scales of primary shoot, first pair being normally transverse, as shown, remainder usually spiral with occasionally a second transverse pair, as in fig. 18; ×24.

VASCULAR FEATURES.—STRASBURGER (**35**) was the first to describe the vascular supply of the primary shoot of *T. baccata*, and it is essentially the same in *T. canadensis*. The primary shoot receives two bundles from the axis of the leafy shoot (figs. 12–15). These bundles meet at their edges (fig. 16) and form a complete vascular cylinder, which then gives off traces to the lateral scales (figs. 17–20). At the level of the fertile scale the cylinder organizes

into two large bundles, which pass into the axis of the secondary shoot (figs. 19–22), only a very weak vascular supply passing into the arrested primary axis tip. If there are two secondary shoots, each receives a pair of vascular bundles (figs. 23–27). Should the primary axis grow out into a leafy shoot the next season, a normal vascular cylinder develops, and the vascular supply to the secondary shoot has the usual features of an axillary structure (figs. 28–30). The normal continuation of the primary shoot in its dwarf character during the next season results in a vascular supply to the new growth, similar to that of the preceding season. The vascular tissue of the new growth develops in connection with the bases of the bundles which passed to the secondary shoot of the preceding season, so that a series of sections shows a continuous vascular strand throughout the entire secondary shoot axis, broken by the small scale traces and by a wide gap at the level of the secondary shoot scar, where the bundle supply to the secondary shoot had passed off from the main axis. This gap, however, does not have the ordinary features of a branch gap, being really the leaf gap of the fertile scale subtending it, the bundle supply of the detached secondary shoot being in lateral connection with the main axis at all points, and not separated from it as in ordinary branch gaps (fig. 32; cf. figs. 13, 14). The previously arrested and rudimentary condition of the axis tip accounts for this behavior. The xylem portion of the cylinder is relatively narrow, growth being slow and uniform. Shoots more than one year old do not usually show any growth ring excepting in the region of the secondary branches of the preceding seasons, where the limit between the xylem of the first and second season's growth is very distinct. The xylem is endarch in the cylinder, but in the scales centripetal wood may appear, although the scale traces in general are quite short, frequently ending in the base of the scale.

Morphological nature.—The morphological nature of the primary shoot has been the subject of some question. It seems clear that in *Taxus* the primary shoot is to be regarded as a vegetative shoot of limited growth, persistent for an indefinite period, producing secondary fruiting shoots season after season, as a dwarf shoot functioning only in this way. It may become a vegetative



FIGS. 19–33.—Figs. 19–22, series showing bundle supply from primary shoot to secondary shoot, also transition from normal primary cylinder (fig. 19) to organization into two bundles supplying secondary shoot (fig. 21); figs. 23–27, series showing vascular supply to two secondary shoots on primary axis; figs. 28–30, series showing vascular supply when primary shoot becomes functionally vegetative second season; two large bundles of figs. 28 and 29 belong to secondary shoot, circle of small bundles to primary shoot; figs. 31–33, series through primary shoot at least two years old, showing: fig. 31, usual primary shoot cylinder; fig. 32, large gap formed by bundle supply to secondary shoot (note that bundle supply to secondary shoot is laterally continuous with primary axis cylinder and has not formed branch gap as for normal axillary structure); fig. 33, through branch scar (with crossed lines), and fertile scale; ×24.

shoot of unlimited growth, however, then having both the vegetative and reproductive possibilities of any other branch. The occasional behavior of the terminal bud in becoming a dwarf primary shoot recalls a similar behavior in *Ginkgo*, although one must not infer too much as to relationship on this account.

Secondary shoot

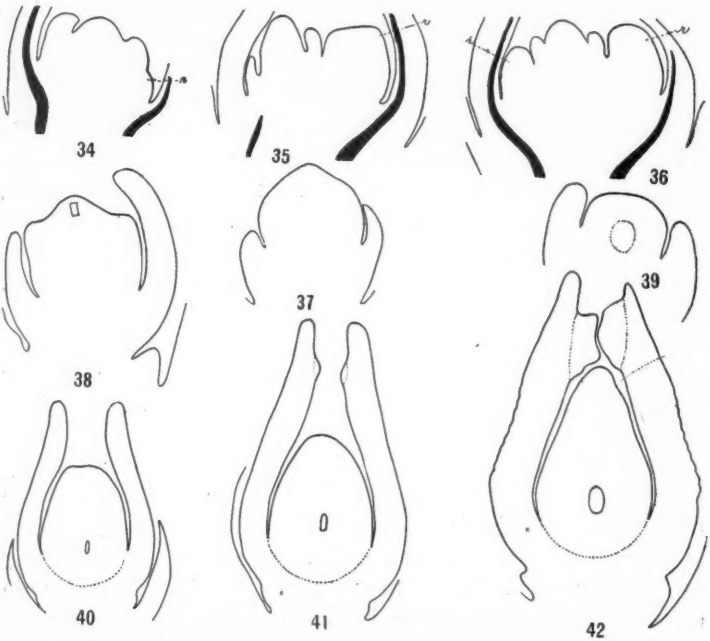
GENERAL FEATURES.—The primordium of the secondary shoot first appears as a lateral structure in the axil of one of the uppermost scales of the primary shoot (fig. 34), soon becoming conical (fig. 35). It is generally stated that the terminal scale is the fertile one, but one or more small scales usually appear above the fertile one, as was pointed out in *T. baccata* by VAN TIEGHEM (**37**). Different writers have assigned definite scales of the primary shoot as the fertile one in *T. baccata*, VAN TIEGHEM claiming the eleventh, STRASBURGER (**36**) the eighth or thirteenth, and PILGER (**23**) the seventh; but this varies and is of no special importance. Frequently two of the scales are fertile and two secondary shoots occur, the tip of the primary shoot then appearing between them (fig. 36). In *Torreya* there are usually two secondary shoots on a primary shoot, but STRASBURGER'S account that in rare cases in *Torreya* the primary shoot behaves as a secondary shoot, and bears a third ovule above the two secondary shoots, does not apply to *Taxus*.

The rudiment of the secondary shoot develops rapidly, producing the three pairs of decussate scales in rapid succession, the cyclic arrangement of which is in contrast with the spiral arrangement of the scales of the primary shoot. The first pair stands transversely to the fertile scale. VAN TIEGHEM held that while the scales are decussate there is an indication of a spiral tendency, a view necessary to his theory that the ovule is an axillary structure of the sixth scale of the secondary axis. Practically all investigators agree as to the decussate nature of the scales, as there seems to be no basis for regarding the scales as having a spiral arrangement. The scales of the secondary shoot are considerably larger than those of the primary shoot, and contain chlorophyll, the outer epidermis being heavily cutinized, and stomata occurring on the inner surface. In the early stages these scales protect the young

ovule, but shortly before pollination the tip of the ovule protrudes from between the scales, and with its development they become relatively less conspicuous.

OVULE

HISTORICAL.—The ovule of *Taxus* has been the subject of considerable discussion among botanists. The earlier taxonomists, such as LINNAEUS (**17**) and JUSSIEU (**16**), regarded the ovule of



FIGS. 34–42.—Fig. 34, long section of primary shoot showing lateral axillary rudiment (*r*) of secondary shoot; fig. 35, older stage, rudiment become conical; fig. 36, rudiments of two secondary shoots, primary axis tip between; fig. 37, axis tip of secondary shoot showing bulge indicating beginning of integumentary zone; fig. 38, older stage showing integumentary zone more distinct and differentiation of archesporium (for detail see fig. 61); fig. 39, older stage showing young integument and position of sporogenous tissue (inclosed by dotted line); fig. 40, young ovule about time of pollination, showing barrel-shaped integument and large open micropyle; figs. 41, 42, older ovules and closure of micropyle by plug tissue (for details see figs. 66, 67); figs. 34–39, ×80; figs. 40–42, ×36.

all conifers as a pistil. TREW's observations, in 1767, that the ovule of conifers receives the pollen directly, the representation of TREW's observations by TARGIONI-TOZETTI in 1810 (RADAIS **24**), and BROWN's (**6**) announcement of gymnospermy introduced a fertile topic for debate. For a time these newer views met strong opposition, RICHARD (**25**), for instance, declaring that there are no plants with naked ovules or without an ovary, and holding that the ovular integument was the perianth and the nucellus the pistil of the flower. BAILLON (**2**) was also a vigorous opponent, holding the ovule to be a 2-carpel ovary with a single orthotropous ovule. PARLATORE (**22**), SPERK (**34**), with others, and even STRASBURGER (**35**) for a time also held to the ovarian theory of the ovule. Another group, among whom were SCHLEIDEN (**29**), A. BRAUN (**5**), SACHS (**26**), and others, accepted BROWN's view as to gymnospermy. STRASBURGER later accepted the same interpretation, and the question of the gymnospermy of *Taxus* has been generally accepted.

The morphological position of the ovule has not been so definitely settled, and it may yet be regarded as an open question whether it is a lateral structure, foliar in origin and only secondarily terminal, or a true terminal structure, unrelated to the scales in its origin. The first of these views depends upon the assumption that the ovule in gymnosperms must always be related to sporophylls, present or suppressed; the second that the ovule may arise from the axis itself, independent of lateral organs. Among the early workers SCHLEIDEN (**30**), SCHACHT (**28**), and others regarded the ovule as terminal to the branch. On the other hand, DON (**11**), CASPARY (**7**), and others held to the foliar origin of the ovule. VAN TIEGHEM (**37**), using the anatomical method as a basis of interpretation, concluded from the orientation of the bundles that the ovule represents the first and only leaf of a shoot of the third order in the axil of the sixth bract of the secondary shoot, a view also accepted by STRASBURGER (**35**). SACHS (**26**) regarded the ovule as secondarily terminal, the bract nearest the ovule playing the rôle of the carpel, but later (**24**) changed his opinion, admitting the ovule to be terminal and a modified stem. STRASBURGER also abandoned his earlier position and held that the ovule is strictly terminal on the axis tip, that no relation to the last pair of scales

can be found, and that there is no ground for VAN TIEGHEM'S view. MAGNUS (18), pointing out the cauline origin of the ovule in *Naias*, spoke of it being similar to the situation in *Taxus*, in which he regarded the ovule as terminal. Later workers have more generally accepted the terminal nature of the structure. CELAKOVSKY (8) held that the sporangium is terminal to the axis. WORSDELL (38) accepted and championed this view, stating that "anatomy points clearly to the fact that no axial foliar appendage of any kind exists upon which the sporangium is inserted, the cylinder of the axis being directly continuous into the base of the sporangium." JÄGER (15) speaks of the nucellus in *T. baccata* being formed by the vegetative tip of the secondary shoot. Miss AASE (1), in a recent study of this problem, points out that the vascular supply to the ovule is "contrary to what should be expected" for an axillary structure. She also suggests the possibility of a fusion of sporophylls to form a single structure.

For a solution of the problem two groups of facts can be used directly, the origin and development of the ovule, and its vascular supply; the latter will be treated in connection with the vascular features of the secondary shoot as a whole. There are no known abnormalities with which one can compare the normal situation. *Torreya* apparently presents a similar situation, and thus gives no additional line of evidence.

ORIGIN OF OVULE.—The first indication of the ovular nature of the end of the shoot is the beginning of the integument as a ring around the tip of the axis (figs. 37, 38), and the axis tip itself becoming the nucellus, as claimed by both STRASBURGER (36) and JÄGER (15) for *T. baccata*. There is nothing in the position of the ovule to indicate that it is a lateral structure, and so far as its ontogenetic origin gives a clue one must conclude that the ovule is strictly terminal, cauline in origin, and unrelated to any of the scales. If the scales represent sterile sporophylls phylogenetically, as is most probable, their sporophyll character has been completely abandoned and the axis itself becomes the sporangium, as in some of the angiosperms, where cauline ovules are not uncommon. That the vascular features sustain this view will be indicated later.

MEGASPORANGIUM.—In *T. baccata* STRASBURGER (**36**) pointed out the hypodermal origin of the archesporium, describing it also for *Larix europea*. In *T. canadensis* the sporogenous tissue is also hypodermal in origin, the archesporium becoming differentiated very early in the development of the nucellus while it is yet cone-shaped and the integumentary zone in a rudimentary condition (figs. 38, 61). It may consist of a single cell or a small plate of cells. The periclinal division of the archesporium results in the primary wall cell and the primary sporogenous cell (fig. 62). The wall cell, together with other adjacent cells of the nucellus, divides repeatedly by periclinal divisions, building up a considerable mass of tissue between the sporogenous tissue and the epidermis, the cells of this tissue being in radial rows, at the inner ends of which are the sporogenous cells (figs. 63–65). Morphologically this is the outer portion of the many-layered wall of the megasporangium, and together with the epidermis constitutes the upper portion of the nucellus. The later development results in a considerable mass of sporogenous tissue (fig. 64), out of which one or more cells function as megaspore mother cells (fig. 65), as pointed out in my previous paper (**12**). While I have no preparations showing divisions of the primary sporogenous cells, the amount of sporogenous tissue present indicates that this takes place, contrasting with the situation in which the primary sporogenous cell functions as the megaspore mother cell, as is probable in most conifers.

GROWTH OF NUCELLUS.—By the formation of the integument the nucellus becomes limited to a knob, at first conical; but with the development of the megasporangium it soon becomes rounded. From the growth of the wall, as just described, there develops a considerable mass of tissue above the sporogenous tissue. At first this tissue seems to be uniformly meristematic, but later division becomes confined to the inner portions, the outer cells and the epidermis becoming radially elongated. I was not able to find any actual periclinal divisions of the epidermis, but the position of the cells in the layers next to the surface (fig. 65) would indicate such divisions as STRASBURGER (**36**) found in the development of the nucellus of *T. baccata*, giving a several-layered epidermis. The nucellus, therefore, is composed of two morphological entities,

the epidermis and the sporangium. The nucellus increases in diameter by anticlinal divisions of both epidermis and sporangium wall. Basal growth takes place also, so that the sporogenous region becomes situated in the focal center of the oval nucellus (figs. 40–42). From this time greater meristematic activity occurs in the peripheral regions contiguous to the line where nucellus and integument meet, resulting in the enlarged base of the nucellus. The tapetal function of that portion of the nucellus immediately surrounding the developing gametophyte, and the digestion of the nucellar tissue in the enlargement of the endosperm have already been described (12). The growing endosperm presses upon and stretches the nucellus so much that at maturity it is but a thin layer surrounding the endosperm.

A feature of interest is the extent of the freedom of the nucellus from the integument. In the earlier stages of development the two structures are entirely free from one another, a condition which persists until about the time of fertilization. The chalazal region now becomes the center of great meristematic activity, resulting in the development of the aril and the zonal growth of nucellus and integument as a united structure, so that at maturity the freedom of the nucellus from the integument is only partial. HOFMEISTER'S (14) statement that in *T. baccata* the separation between the "nucleus" (nucellus) and the integument extended entirely to the base was most probably based on young ovules. Freedom of nucellus and integument occurs in Paleozoic seeds belonging to the Cordaitales, such as *Cordianthus*, and is perhaps a primitive feature retained by most modern gymnosperms only during the early stages in the development of the ovule. That freedom of the two structures should persist longer in some forms than in others is not surprising, and has been regarded as having morphological significance. *Taxus*, *Torreya*, and some others are alike in retaining this feature for some time, the relative amount of it being correlated somewhat with the size of the seed, basal growth of the ovule being more extensive in some forms than in others. OLIVER (21) has called attention to the basal intercalary growth of the ovule in *Torreya*, which results in raising both nucellus and integument. He also suggests that the lower portion

of the seed is phylogenetically younger than the apex, where nucellus and integument are free from one another, introducing a problem already suggested by STRASBURGER (**36**) as to the real limits of the morphological ovule.

INTEGUMENT.—The development and structure of the integument of *T. baccata* have been described rather completely by STRASBURGER (**35**), BERTRAND (**3**), and JÄGER (**15**), and are not different in *T. canadensis*. The integument arises as a zone of meristematic tissue surrounding the young nucellus (figs. 37–39). Uniform growth in the entire zone results in a cylindrical, barrel-shaped integument surrounding the young nucellus (fig. 40), and extending some distance above it. At first the integument is uniform in thickness, six or more cell layers thick. The integument is 2-lipped from the early stages in its development, the lips alternating with the upper pair of scales. This feature has led some workers to interpret the integument as two carpels, and others as the fusion of two sporophylls. This 2-lipped character persists to the mature seed, but probably has no more morphological significance than has a similar and more pronounced feature in the ovules of many other conifers, especially the Abietineae, in which no foliar significance is attached to this character.

Up to the time of pollination the micropyle is relatively large (fig. 40). At pollination it is filled with the pollination droplet. At this time the inner wall of the integument is smooth, but soon after pollination becomes closed by the centripetal radial growth of a portion of the inner epidermis of two sides (figs. 41, 42, 66, 67). Closure of the micropyle in this way takes place even if the ovule is not pollinated, my preparations showing no difference in this respect between pollinated and unpollinated ovules. JÄGER found cases in *T. baccata* in which the micropyle had not yet closed at the time of fertilization, although usually taking place soon after pollination. In *Juniperus* both NORÉN (**20**) and NICHOLS (**19**) claim the failure of micropyle closing unless pollen of *Juniperus* has entered it, foreign pollen having no effect. Experimental data on this point would be of interest. It would seem that the pollination droplet would be a more likely growth stimulant in this region than the presence of a pollen grain on the somewhat distant nucellus,

or of pollen tubes within the nucellar tissue. JÄGER also speaks of a ring-formed thickening at the outer end of the micropyle, a feature not present in *T. canadensis*.

In its later development increase in thickness occurs below the tip region, while growth in length is largely the result of chalazal activity. In cross-section the young ovule is practically circular in outline, but as it develops it becomes more elliptical, and, especially in the upper portions, pronouncedly 2-ridged, the ridges corresponding with the lips. Frequently there are three ridges, occasionally four, the 2-lipped character, however, remaining constant. STRASBURGER records finding very rare cases of 5-ridged integuments. These ridges have been regarded as the midribs of fused sporophylls, but, as shown later, are associated with the vascular supply of the ovule and do not necessarily indicate a sporophyll character of the integument.

The histology of the integument has been accurately described for *T. baccata* by both STRASBURGER (**35**) and BERTRAND (**3**), a description which will also hold for *T. canadensis*. Before the hardening of the seed coat the following regions (fig. 68) are to be recognized: (1) the outer epidermis of large papillate cells, covered with a very heavy cuticle; (2) the hypoderm, large thick-walled cells, which become filled with brownish-red contents and give color to the seed coat; (3) a sub-hypodermal layer of small radially elongated cells; (4) a thick tissue of small irregular cells, extending to the inner epidermis, next to which the cells are longitudinally elongated; and (5) the inner epidermis, which in the micropyle region forms the plug tissue (fig. 67), and below, as far as free from the nucellus, consisting of elongated thick-walled cells containing a dark staining material. Below the union of the nucellus and integument the boundary between the two is not distinct. Large secretory cells are abundant in the inner tissue, and along the 2-keeled sides the strands of vascular elements traverse the integument. Formation of the stony character of the seed coat begins at the apex and extends downward, involving all the tissue of the integument excepting the epidermis and hypoderm, the cells becoming "stony," with very thick walls pierced by protoplasmic connections (fig. 69). The hardening begins very soon

after fertilization, and by seed maturity has reached the base of the seed. In the meantime the aril has developed, surrounding the hard nutlike seed.

ARIL.—In the young ovule there is no indication of the aril, but about the time of pollination the aril primordium begins to develop as a ring at the base of the ovule (fig. 40). Its early development is contemporaneous with the chalazal growth of the ovule. In its early stages it is a flat saucer-shaped structure (figs. 5, 11) of greenish color and of slow growth until the seed is nearly matured and the seed coat hardened. Then there is very rapid growth; it soon becomes cup-shaped and reaches its mature condition, that of a large red fleshy cup inclosing the hard seed (figs. 8, 43). The chalazal portion is a tissue of small cells, traversed by the vascular elements which supply the hard integument. The sides of the aril consist of very large delicate-walled cells, filled with a watery material, the long cells being extended radially and obliquely upward. The epidermis is a narrow layer of small pigmented cells, and contains fairly numerous stomata, oriented longitudinally.

The morphological nature of the aril has been one of the mooted questions in the taxads, having been regarded as: (1) a special outgrowth surrounding the ovule, (2) a carpel, (3) representing the ovuliferous scale of other forms, (4) a second (outer) integument, and (5) the fleshy layer of a single integument. RICHARD (25) regarded the aril as the equivalent of the collar of *Ginkgo*, an accessory structure formed from the flower stalk. BLUME (4) thought of it as a carpel, and BAILLON (2) as an expansion of the axis surrounding the ovary. PARLATORE (22) seems to have been the first to regard the aril as the morphological equivalent of the ovuliferous scale of other forms, a view followed by CELAKOVSKY (8) and WORSDELL (39), both claiming the ovuliferous scale of conifers to be the morphological equivalent of the "epimatium" of the podocarps, of the outer fleshy layer of the ovule of *Torreya* and *Cephalotaxus*, and of the aril of *Taxus*. SINNOTT (33), in his study of the podocarps, holds a similar view with reference to *Cephalotaxus*, the logic of which would be to regard the aril of *Taxus* in the same light. STRASBURGER (35), with BAILLON (2), regarded the aril

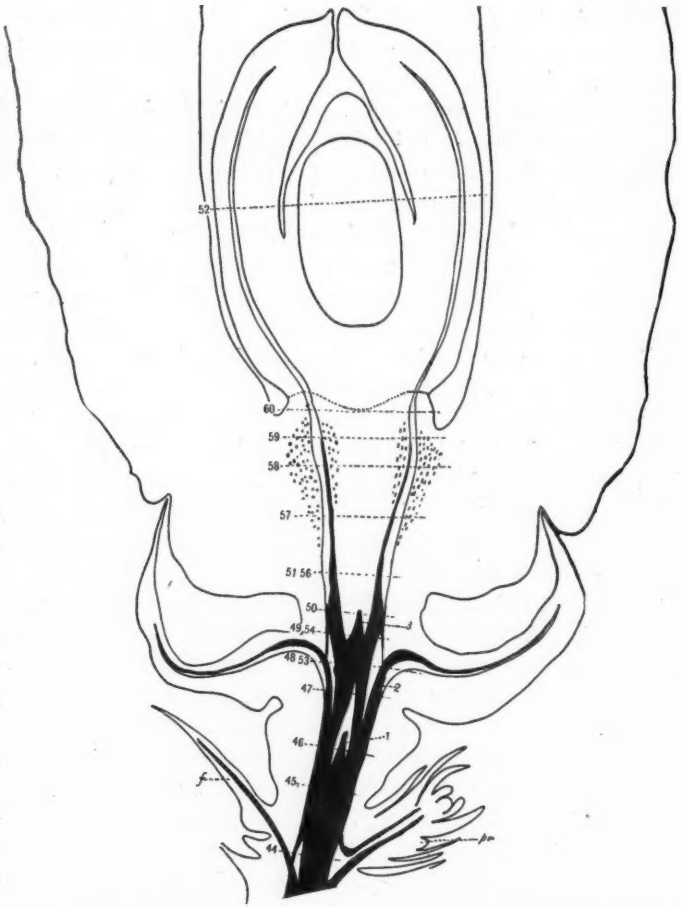


FIG. 43.—Semi-diagrammatic longitudinal section through primary shoot with secondary shoot and portion of mature ovule, ×17; outlines of primary and secondary shoots and aril of ovule made with camera lucida, ovule inserted diagrammatically; outlines of vascular supply also made with camera; note young ovule of next season above primary axis tip (*pr*); *1*, *2*, *3*, traces to 1st, 2d, and 3d pairs of scales, second pair of which shown in section; *f*, fertile scale of primary shoot; whole vascular cylinder of secondary shoot shown in black, light portions showing gaps in cylinder formed by scale bundles; in base of aril and seed, relation of xylem and phloem shown as seen in long section, xylem black, phloem white; scattered tracheids described are shown by area of black dots; curved line at base of seed shows line of separation when seed is removed from aril, and limit of camera outline of slide from which drawing was made; figures at ends of dotted lines across vascular tract indicate cross-section drawings corresponding to these levels.

as an outgrowth of the axis, discoid in nature, a view also held of the ovuliferous scale of other forms. BERTRAND (3) and SCHUMANN (31) both held the aril to be a special structure, the former regarding it as a proliferation of the cortical parenchyma at the base of the integument (which he regarded as the equivalent of the ovuliferous scale). JÄGER (15) regards the aril as a second or outer integument, basing his argument on the similarity in origin of the integument and the aril.

It will thus be seen that the structure is one which has given considerable difficulty in its interpretation, some of the explanations being perhaps more ingenious than reasonable. The carpellary nature of the aril no longer held sway after the acceptance of the gymnospermy of *Taxus*. That the aril may be a special structure arising from the axis and having no morphological significance seems an unnecessary way of avoiding the problem, and while possible is hardly probable. The view which regards it as equivalent to the ovuliferous scale of other forms has more in its favor, the chief objections to the idea for *Taxus* being the cauline origin of the ovule, independent of any recognizable sporophyll, and the belated appearance of the structure. It is hardly reasonable for the ovule to be present for so long and to reach such an advanced stage in development before the appearance of the structure on which it is supposed to be produced. Accepting the aril of *Taxus* and the fleshy layer of *Torreya* and *Cephalotaxus* as homologous structures, there is involved the difficulty of explaining why the aril should be free in one form and organically attached in the others, if representing the ovuliferous scale in all. The entire absence of a vascular supply in the aril of *Taxus*, excepting the strands which pass through its basal portion, makes impossible an interpretation based on its vascular features.

The question of two integuments or one seems to be partly a matter of terminology. Distinction needs to be made between the idea of two integuments, an inner and an outer one, and the idea of a single integument of three layers, the outer fleshy one of which may be more or less free from the other two. COULTER and LAND (10) have described the situation in *Torreya taxifolia*, and speak of the outer fleshy layer of the ovule as the outer integument. Concerning *Torreya*, COULTER and CHAMBERLAIN (9) state

that "it is a natural thing to see in these three layers characteristics of the testa in cycads, *Ginkgo*, and the older gymnosperms; and to conclude that the two integuments have arisen from a single one by delaying the development of the region that becomes the outer fleshy layer. These facts and the inference seem to hold good also in the case of *Taxus*, the only difference being that the outer fleshy layer (aril in this case) remains distinct from the inner one." In *Taxus* this freedom of the aril and hard integument extends to the base (fig. 43), probably due to the fact that the development of the aril begins relatively late. COULTER and LAND'S figure of the ovule of *Torreya* at the mother cell stage shows considerable growth of the fleshy layer, while a corresponding stage (fig. 40) in *Taxus* shows but the beginning of the aril primordium. In *Torreya* there is a much greater and earlier chalazal growth of the ovule, resulting in a larger seed than in *Taxus*, the bulk of which is produced below the point of juncture of the fleshy layer and the hard coat.

In *Taxus* the inner fleshy layer may be represented only by the inner epidermis, and possibly a few layers of cells in the basal portion of the ovule, and is practically absent. The remainder of the seed coat becomes hardened, with the exception of the epidermis and hypoderm. It hardly seems reasonable to regard these two layers of cells as representing the outer fleshy layer, but rather that their failure to develop the stony character is due to their superficial position. "The probability is that the stony layer would not develop superficially in any event, so that it would not be necessary to regard a layer or two of cells overlying it (the hard coat) as representing the outer fleshy layer (COULTER and CHAMBERLAIN **9**, p. 418). The inference is that the outer fleshy layer is lacking in the Pinaceae, and from the same reasoning the outer layer of the seed coat in *Taxus* need not be regarded as an outer fleshy layer. Even the claim for two integuments in the old Cordaitean seeds is based on weak evidence, and the seed coat there "may correspond to the outer fleshy layer and stony layers of the single integument of cycads and *Ginkgo*" (COULTER and CHAMBERLAIN **9**, p. 174). SCOTT (**32**) also calls attention to the possibility of this view. It is likely that only a single integument

occurs in all known gymnosperms, excepting the Gnetales. In the older forms it is more or less distinctly differentiated into the three layers; in the modern forms one or more layers become "reduced," as the outer fleshy layers in most conifers and the inner fleshy layer in such forms as *Taxus*. On the other hand, the taxads are pronounced in the retention of the outer fleshy layer, *Cephalotaxus*, *Torreya*, and *Taxus* showing an excellent series both in the delay in appearance and in the freedom from the stony layer, *Taxus* showing both these features in greatest degree.

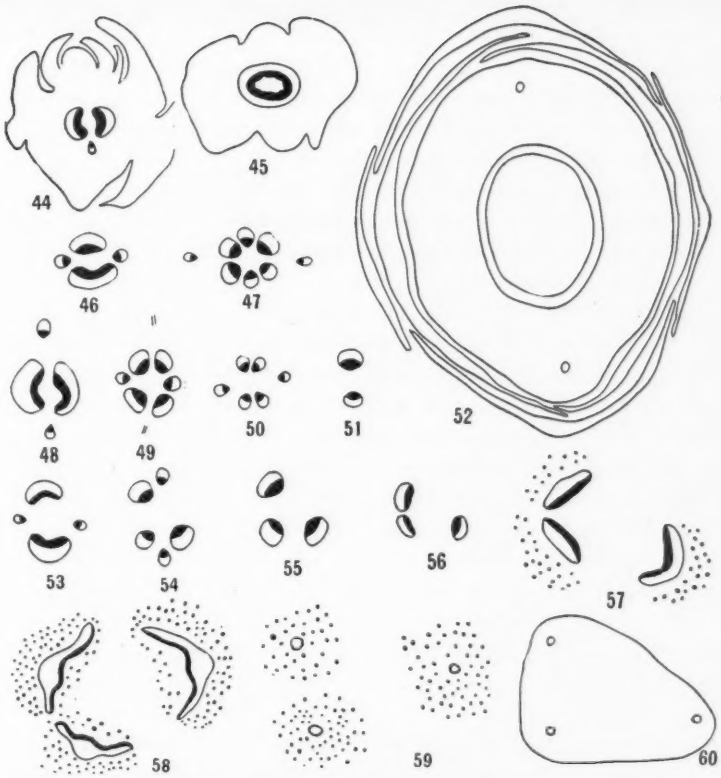
Attempts have been made to relate the taxads to the cycads on account of the fleshy character of the ovule, regarding *Cephalotaxus* and its relatives as bridging from cycads to conifers. The cycadean origin of the conifers does not harmonize with the known facts, however, and the attempt to relate all gymnosperms with fleshy seeds in a common phylogeny is almost as absurd as to attempt to construct a human "family tree" on the same basis. The tendency to "fleshiness" is too scattered to have any phylogenetic significance in a broad sense, although it probably has value within the narrower limits of small groups.

Vascular features

The vascular supply of the secondary shoot of *T. baccata* has been described by Van Tieghem (37), Strasburger (35, 36), and Miss Aase (1). Van Tieghem was the first to apply anatomical criteria to the morphological nature of the ovule, and concluded from the origin, orientation, and structure of the vascular supply that the ovule is a lateral structure, representing the first and only leaf of a branch of the third order arising in the axil of the "sixth scale" of the secondary shoot. According to his description, after the fertile scale has received its vascular supply, two bundles leave the axis, turn in such a way that the xylem is oriented outward, and these two bundles then penetrate the ovule, where, after forming a "small vascular cup," they give off, ordinarily two, sometimes three, or even four or five, branches into the integument. He also gave the bilateral symmetry of the ovule as one of the reasons for regarding it as axillary, bilateral symmetry being characteristic of leaf structures as contrasted with stem

structures. STRASBURGER (35) described the bundle supply to the three pairs of decussate scales and to the ovule, accepting VAN TIEGHEM's interpretation of the situation. Later he reversed his earlier view and regarded the ovule as terminal, there being nothing in the course of the bundles to give a clue to the lateral position of the ovule. He described the bundles in the integument as consisting of long, thin-walled elements, but containing no tracheids. Miss AASE describes the vascular supply to the ovule and the fusion in pairs of the four bundles from the axis as different from cases in which the united bundle is to supply an axillary structure, the pair consisting of "one bundle from each side of the bract bundle of the next lower pair, and not one from each side of the bract of the last pair." Miss AASE also pointed out the concentric character of the bundles in the base of the ovule, and the possible ending of one of the bundles before reaching the ovule. From her study the suggestion is made that there may have been a fusion of sporophylls to form a single structure, implying "the reduction of the ovules to one, the complete fusion of two sporophylls to the integument of the ovule, and finally the reduction of the vascular supply to each sporophyll to the single weak bundle in the wing of the ovule." She concludes, however, that "further investigation is necessary."

In *T. canadensis* the essential facts are not materially different from those of *T. baccata*, and a brief statement of the situation will be sufficient. The secondary axis receives two large bundles from the cylinder of the primary shoot (figs. 21, 44), these uniting at their edges and forming a closed cylinder (fig. 45). The traces to the first pair of scales are given off near this level (fig. 46). Traces are then given off to the second pair of scales (fig. 47), above which the gaps formed by the first pair of traces are closed, giving again two large bundles in the cylinder (fig. 48). The bundles to the third pair of scales are given off directly above those to the first pair (fig. 40), these bundles being usually quite short, at times not even reaching to the scale, but ending in the cortex itself. The main cylinder now consists of four bundles, two on each side, the pairs being separated by the gaps formed by the third pair of scale bundles. The two bundles of each pair turn through an angle of 45° and unite laterally (fig. 51), closing the gap formed by the second



FIGS. 44–60.—Figs. 44–52, series of transverse sections through young ovule (about age shown in fig. 11) showing normal vascular situation at various levels, corresponding to dotted lines figured in mature ovule of fig. 43; fig. 44, two bundles from primary shoot; fig. 45, closed cylinder; fig. 46, bundles to first pair of scales; fig. 47, bundles to second pair of scales; fig. 48, cylinder above second pair of scales; fig. 49, bundles to third pair of scales; fig. 50, cylinder of four bundles in base of ovule; fig. 51, two bundles resulting from pairing of four cylinder bundles; fig. 52, cross-section of young ovule, showing two vascular strands in integument and cyclic arrangement of three pairs of scales; ×24.

FIGS. 53–60.—Series of sections through mature secondary shoot and base of aril showing vascular supply to 3-ridged integument and relation of xylem and phloem in mature condition (note corresponding levels in fig. 43); fig. 53, bundles to second pair of scales; fig. 54, to third pair of scales, one of four bundles of normal cylinder lacking; figs. 55–57, each of three bundles remaining distinct, becoming broader tangentially at higher levels, and in fig. 57 showing scattered tracheids outside phloem; fig. 58, concentric bundle with narrow zone of continuous xylem next to phloem; fig. 59, concentric bundle consisting of small phloem strand surrounded by scattered tracheids; fig. 60, three phloem strands as they pass from aril to seed; ×24.

pair of scale bundles. At the base of the ovule there are then but two bundles, with xylem and phloem in normal position, and not showing the inverse orientation claimed for *T. baccata* by VAN TIEGHEM. Miss AASE'S figures of *T. baccata* also show normal orientation at this level. These two bundles become more widely separated and enter the integument at opposite sides (figs. 43, 52), whence they traverse the integument almost to the tip of the ovule, their position being indicated externally by the ridges on the integument. As Miss AASE pointed out, one of the four bundles may terminate before reaching the base of the ovule (figs. 53–56), in which case the odd bundle may behave in the same way as the fused bundle. Ovules with three or four vascular bundles in the integument occur with some frequency, such situations occurring as a result of the failure of the fusion of one or both bundles, in which case each bundle is continued into the integument (figs. 53–60). Frequently when one of the four bundles of the normal cylinder is absent (figs. 54, 55) a 3-ridged integument results, no fusion taking place, but each bundle remaining distinct (figs. 53–60).

At the level of fusion the bundles are oval (fig. 51), and the fusion bundle remains this shape for some distance into the chalaza of the ovule. At a higher level they begin to widen laterally (figs. 57, 58), whether fusion has taken place or not, until near the upper level of the chalaza they reach their greatest width, both radially and tangentially. They then suddenly become narrow, and pass into the hard integument as narrow strands (figs. 43, 60). The bundles are endarch throughout their course, and at the base of the aril are collateral. Higher up, however, scattered xylem elements, consisting of short spiral-marked tracheids with bordered pits, appear outside the phloem (figs. 57, 58), and in the upper portions of the aril base the bundles consist of the phloem strand surrounded on all sides by the loosely distributed short tracheids (fig. 59). The tracheids occur only in the aril portion of the chalaza, the bundles as they pass into the integument consisting only of few thin-walled elements of phloem tissue.

It would seem that the vascular supply to the ovule favors the interpretation of it as terminal and cauline in nature. The vascular

supply arises equally from the two sides of the axis cylinder, the entire cylinder being involved in the supply. The bundles as they pair and fuse arise from opposite the second pair of scales and alternate the third pair of scales, an anomalous situation if the ovule were axillary to either of the third pair of scales. The ovule bundle supply is a direct continuation of the axis cylinder, the fusion of the bundles in the base of the aril closing the gap above the second pair of scale bundles. The orientation of the bundles is normal and presents no difficulty. The course of the bundles being opposed to the idea of an axillary origin is also against the view that there may have been a fusion of sporophyll with integument, and that the integumentary bundle is a vestige of that fusion. The presence of vascular bundles in the integument of gymnosperms is sufficiently common to cause no surprise in such forms as the taxads, nor is there any more argument for the sporophyll nature of the integument there than there might be in the cycads, where sporophyll and ovular integument are not confused, unless it be necessary to supply a theoretical sporophyll for a terminal cauline ovule.

The terminal cauline nature of the ovule is a much simpler interpretation of the facts, according both with the ontogenetic origin and the vascular supply. While this is an unusual situation for a gymnosperm, it is not out of harmony with a tendency among the seed plants, a tendency expressing itself frequently in angiosperms and not necessarily impossible in gymnosperms.

Summary

1. The ovuliferous bud arises in the axil of a leaf early in the season, and matures the next year.

2. The ovuliferous organ consists of the primary shoot and the secondary shoot with the ovule.

3. The primary shoot is to be regarded as a vegetative branch of limited growth, bearing only reproductive axes (secondary shoots). While of limited character, at times it may become a functional vegetative shoot like any other vegetative branch.

4. The primary shoot is a persistent structure, functional for several successive seasons.

5. Occasionally the primary shoot may be terminal to a leafy branch.

6. The secondary shoot consists of three pairs of decussate scales and a terminal ovule.

7. The ovule arises as a direct continuation of the axis, there being nothing in its origin to indicate that it is a lateral structure.

8. The archesporium arises from the hypoderm. The sporogenous tissue consists of a considerable mass of cells, out of which one or two may function as megaspore mother cells.

9. The aril is regarded as the morphological fleshy layer of a 3-layered seed coat, delayed in appearance and physically separate from the hard stony layer.

10. The ovule receives its vascular supply direct from the axis cylinder, contrary to any axillary nature, and in harmony with the view that it is a cauline structure.

The writer acknowledges obligations to Professors JOHN M. COULTER and CHARLES J. CHAMBERLAIN, under whom the study of *Taxus* was begun.

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EXPLANATION OF PLATE XXIII

All figures were made with a camera lucida excepting figs. 2, 4, 8, 10, and part of 43. Text figures have been reduced to one-third and plate figures to one-half original size. The scale of magnification of the figures is shown in connection with the descriptions.

FIG. 61.—Archesporial initial showing hypodermal position; ×475.

FIG. 62.—Two archesporial cells divided, each forming primary wall cell and primary sporogenous cell; ×475.

FIG. 63.—Primary wall cells divided and beginning formation of megasporangium wall; ×475.

FIG. 64.—Older nucellus showing several-layered wall and central mass of sporogenous tissue (detail of fig. 39); ×475.

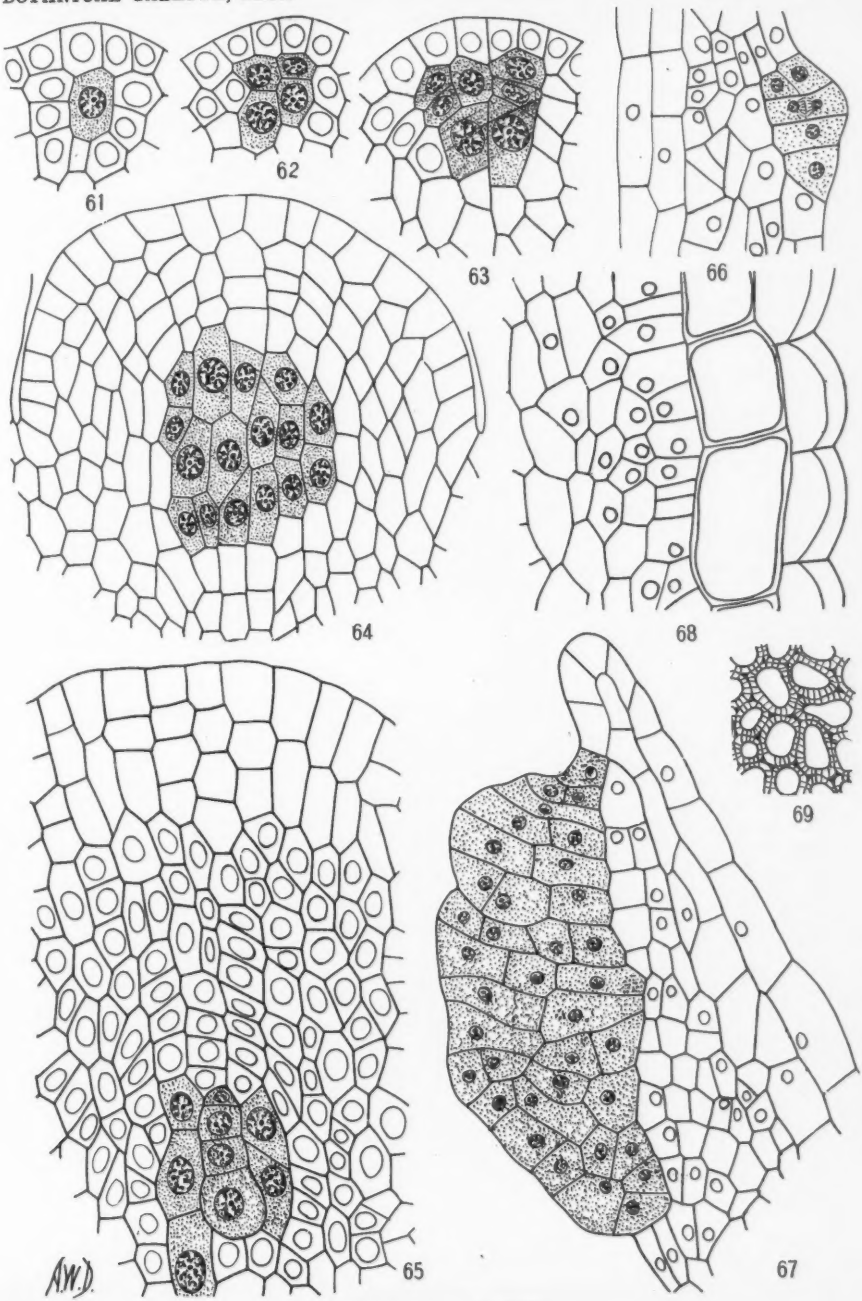
FIG. 65.—Portion of nucellus showing several-layered epidermis (cells without nuclei), megasporangium wall (cells with nuclei), and sporogenous tissue (shaded) with group of megaspores; ×475.

FIG. 66.—Portion of integument showing beginning formation of plug tissue; ×210.

FIG. 67.—Mature plug tissue; ×210.

FIG. 68.—Detail showing integumentary regions, outer papillate epidermis with heavy cuticle, hypoderm of large cells, sub-hypodermal layer, and internal tissue; inner epidermis not shown; ×210.

FIG. 69.—"Stony cells" from hard integument showing protoplasmic connections; ×210.



DUPLER on TAXUS

ROT OF DATE FRUIT[1]

J. G. BROWN

(WITH FIVE FIGURES)

In the autumn of 1917, Dr. A. E. VINSON of the Arizona Experiment Station brought to the writer a small box of dates from the Yuma date orchard with the request that the organism with which they were badly infected be determined. The fruits were carefully examined, but it was impossible to give the requested information without further investigation; and it was suggested by Professor THORNBER, Botanist of the Station, that since the problem concerned food conservation it would be especially profitable to attack it at once. The advice was acted upon, and the results are partly set forth in this preliminary paper.

For the purpose of observing the disease in the field, a trip was made to the orchard in December 1917, and a careful inspection of trees and fruit was undertaken. A glance at the figures will show that abundant evidence of disease was not difficult to find. The ground under many of the trees was thickly covered with the spoiled fruit (fig. 1), and numerous clusters still hanging to the trees suggested a severe attack of "plum pockets," for a large percentage of the fruit had become mummified (fig. 2). Some of the fruit on the ground was covered with molds, and similarly infected fruit was found wedged between the leaf bases and tree trunks and on the ground half buried in the soil. Of the several varieties of date palms comprising the orchard, the Deglet Noor appeared to be the favorite host. It was stated that the year had been an especially bad one, about 90–95 per cent of the crop being infected. The fruit was selling at the orchard at 35–45 cents per pound. Since many of the trees produce from 200 to 400 pounds of salable fruit under normal conditions, the loss was considerable.

Both Yuma and Tempe date orchards were affected much less by the rot in 1918 than in 1917. Table I gives precipitation and

[1] Preliminary paper.

FIG. 1.—Deglet Noor variety showing ravages of date rot disease; note mummies still hanging to tree and on ground.

FIG. 2.—Various stages of date rot and mummification

temperature data for the Yuma date orchard covering the two years. Table I suggests that the greater prevalence of the fungi concerned in the rot of the date fruit in 1917 was possibly due to the more favorable conditions of moisture and temperature during April, May, and June, while flowering and fruit setting were in progress. From observations it appears probable that infection occurs at that time. The spring and summer of 1917 had not only an excess of moisture over the same period of 1918, but were also cooler, so that this additional moisture was more effective.

SYMPTOMS.—The fruits showed two main symptoms. Some were flecked with rusty brown spots from the size of a pinhead to areas almost covering one side of the fruit (fig. 4); others showed soft spots varying in size and partly translucent, as though soaked with water or oil (fig. 5). The brown spots gradually increased in size, often coalescing, forming a dark chocolate margined area oval in outline, with depressed, light cream or grayish centers on which clusters of spores finally appeared in pustules (fig. 4, third fruit, third row). The soft spots also enlarged to a similar extent, giving an appearance of rot. In both cases the ruptured epidermis allowed excessive water loss, resulting in the final mummy stage. Mummified fruits sometimes remained for a time in situ, but sooner or later fell to the ground (figs. 1 and 3). The exposed sweet pulp, in the early stages of the soft spots, attracted swarms of small flies and other insects which hovered in and around the fruit clusters, and probably aided materially in carrying the infection.

Examination of the trees revealed numerous brown spots on petioles and ribs of leaves, which also extended down the rhachi of fruit clusters. This suggested a relation between fruit spot and leaf spot, which appears to be confirmed by the laboratory experiments so far completed. In the Tempe date orchard palms three years old already showed the brown spots on the leaf bases.

LABORATORY STUDIES.—Cultures have been made from the spots on leaves, rhachi, and fruits collected in both orchards. The medium used was date agar, prepared according to the method described by SHEAR and STEVENS[2] for prune agar by substituting

[2] SHEAR, C. S., and STEVENS, N. E., Bur. Pl. Ind. Circ. no. 131.

FIG. 3.—Cluster of date fruit from left side of tree shown in fig. 1, showing most of fruit fallen, owing to attack of spot and rot fungi.

TABLE I

	January	February	March	April	May	June	July	August	September	October	November	December
	Comparative precipitation 1917											
Precipitation in inches	.....	.....	∞	0.27	0.05	∞	0.93	0.24	0.18	∞	∞	∞
Departure from normal	.....	.....	−0.26	+0.20	+0.05	−0.06	+0.59	−0.64	+0.09	−0.24	−0.27	−0.41
	1918											
Precipitation in inches	0.62	0.15	0.63	∞	∞	∞	∞	0.39	∞	0.15	0.12	0.27
Departure from normal	.....	.....	+0.37	−0.07	∞	∞	−0.34	−0.49	−0.09	−0.09	−0.15	−0.14
	Comparative temperatures 1917											
Temperature	53.3	.....	59	65.7	69.2	81.2	88.4	86.6	84.2	74.4	60.3	56.6
Departure from normal	.....	.....	−1.5	+0.01	−1.5	+2.8	+2.4	+0.5	+4.9	+6.2	+1.5	+6.3
	1918											
Temperature	53.3	56.7	64.8	68.4	71.8	86.2	87.9	.....	83.7	73.6	58.6	51.6
Departure from normal	+1.6	+1.1	+4.3	+2.8	+1.2	+ 7	+1.9	.....	+3.7	+4.5	−0.3	+ .7

FIG. 4.—Progressive stages in mummification of date fruit, due to spot fungus; spots rusty brown at first, then dark chocolate to black, margined with lighter depressed centers.

dates for prunes. Infected spots in all three situations gave typical *Alternaria* spores similar to those found in pustules. Besides this fungus, two species of *Aspergillus* and one species of

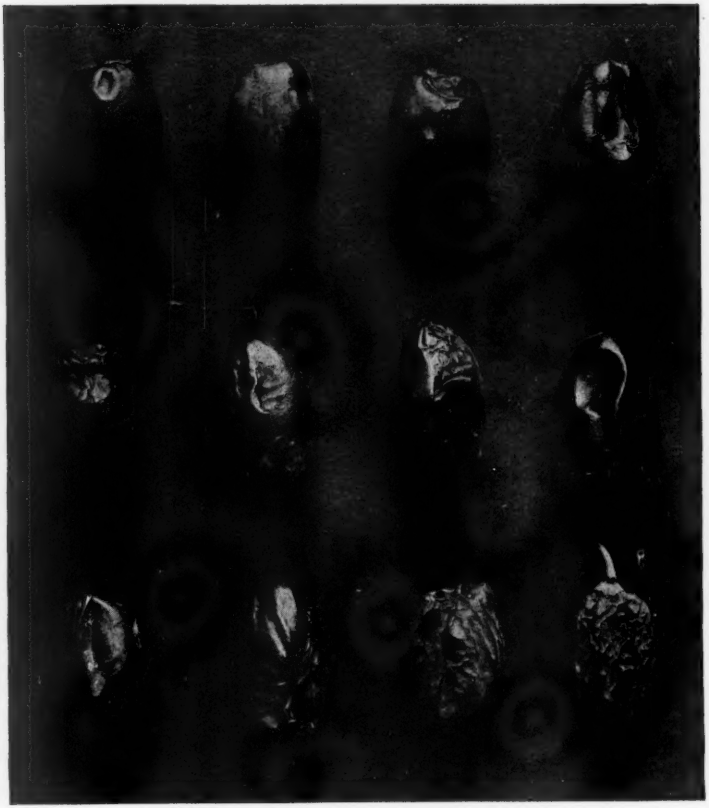


FIG. 5.—Stages in rotting and drying out following attack of *Alternaria*, *Aspergillus*, and *Penicillium*, showing spots having a water-soaked appearance at first.

Penicillium usually appeared. The method of inoculation consisted in the removal of a block of infected tissue with a flamed scalpel after sterilization of the surface. The fungi appearing on the agar have all been isolated and grown in pure culture. On old

agar cultures numerous perithecium-like, carbonaceous structures have appeared, which are now under histological and physiological investigation. In no instance, thus far, have they produced spores on artificial media, nor do they appear on infected material that has been examined.

An important phase of the date rot problem is the difficulty with which stored fruits are kept. Since another investigator is working on methods of preserving date fruit, it will suffice to state that the same saprophytic molds that occur in infected petioles, rhachi, and fruits on the tree are likely later to ruin the packed crop.

CONCLUSIONS.—From the writer's preliminary observations and experiments, it appears probable that the primary cause of rot and mummification of the date fruit is the attack of *Alternaria*. This attack paves the way for the entrance of saprophytic *Aspergillus* and *Penicillium* species which bring on the disintegration of the pulp. Commonly all three fungi appear in cultures from the same infected spot. Attack of the spot fungus, unaccompanied by the saprophytic *Aspergillus* and *Penicillium*, results in mummification without the appearance of rot.

LITERATURE.—There appears to be no literature available on diseases of the date in this country, a statement borne out by communications from the Bureau of Plant Industry. Some European investigators have mentioned a species of *Sterigmatocystis* as the cause of the rot of date fruit in Africa, but this fungus has not yet appeared on any of the Arizona material examined. *Meliola* has also been mentioned in connection with the spot of the leaf of date palms, but it also is absent from cultures made in this laboratory. Further study is needed to determine the species of *Alternaria*, *Aspergillus*, and *Penicillium* isolated in cultures. This work, together with histological investigation and inoculation experiments, is already under way, and it is hoped that a further report may be ready soon.

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CURRENT LITERATURE

BOOK REVIEWS

Inbreeding and outbreeding

The latest of the series of "Monographs on Experimental Biology" is by EAST and JONES.[1] The book is noteworthy in bringing together in convenient form critical data on an important subject, which have heretofore been neither well organized nor readily accessible. Some will object to certain conclusions, but they enhance the value of the book as a monograph, and all assertions are supported by striking evidence.

Chapter i describes the nature of the problem, discusses its sociological, agricultural, and evolutionary significance, and emphasizes the necessity of proper experiments for its solution. Chapter ii outlines briefly the position of cross-fertilization in the evolution of reproduction in plants and animals. The conclusion is that those organisms which were able to cross with others, at least occasionally, have dominated the organic world. For DARWIN's negative proposition, "Nature abhors perpetual self-fertilization," a positive substitute is provided in, "Nature discovered a great advantage in an occasional cross-fertilization."

Chapter iii is a very condensed description of the rôle and behavior of chromosomes in plant and animal reproduction. Sex determination and sex linked inheritance are also included, although the reviewer doubts whether these are necessary. Chapter iv presents MENDEL's law, wisely using a 1:2:1 ratio as the type illustration, linkage, and the factor hypothesis, with particular emphasis on the inheritance of quantitative characters. The rôle of the factor as a mathematical concept, similar to the chemical atom, is ably presented. Chapter v discusses mathematically the effect of various types of inbreeding upon the heterozygosity of a population. Chapter vi presents the inbreeding experiments of CRAMPE, RITZEMA-BOS, WEISMANN, VON GUAITA, KING, ROMMEL, CASTLE, WHITNEY, and A. F. SHULL on animals, and of DARWIN, G. H. SHULL, and of the authors themselves on plants. The emphatic conclusion is that inbreeding is not injurious merely by reason of the consanguinity; apparent evil results are due merely to the isolation of certain recessives.

Chapter vii describes the experiments of KOLREUTER, KNIGHT, GARTNER, NAUDIN, MENDEL, FOCKE, DARWIN, EAST and HAYES, ROBERTS, COLLINS and KEMPTON, GERNERT, and SARGERET on hybrid vigor in plants.

[1] EAST, E. M., and JONES, D. F., Inbreeding and outbreeding. 8vo. pp. 285. *figs. 46*. Philadelphia: J. B. Lippincott Co. 1919. $2.50.

The results involved increase in size (number as well as size of cells), weight, yield, early flowering, longevity, resistance to climate and disease, seed viability, and ease of vegetative propagation. Foreign pollen immediately produces larger endosperm (maize) than does own pollen in different seeds of the same ear.[2] No selective fertilization in favor of foreign pollen is associated with hybrid vigor.[3] Those characters which are quickest to be modified by external factors also show the greatest degree of hybrid vigor on crossing. On hybrid vigor in animals, which is less noticeable, the work of CASTLE is described, and that of some others briefly mentioned. Chapter viii sketches in historical sequence the theoretical mechanisms which have been provided to explain hybrid vigor, culminating with the junior author's explanation through "dominance of linked factors."[4] The faint possibility of fixing "hybrid" vigor is discussed. Chapter ix discusses the relation of the problem to sterility. Two distinct types of sterility occur: (1) inbreeding may isolate sterile strains in the same way that it isolates other characters; and (2) rather wide crosses may produce a sterile F_1 because through the degree of difference between the uniting germ plasms "the precise and complex machinery governing gametogenesis cannot do its work in the normal manner, and sterility results, although under the same conditions developmental (somatic) cell division goes on as usual."

Chapter x sketches the rôle of inbreeding and outbreeding in evolution. It contains a number of interesting speculations, among which the most striking are that hybrid vigor may be pictured as the efficient cause of the establishment of the sex habit itself, and of the rise of the sporophyte generation in plants. The authors differ from many geneticists in claiming that "bud variations occur much more frequently in heterozygotes than in homozygotes." Chapter xi outlines the value of inbreeding and outbreeding in plant and animal improvements. "There must be cross-breeding to furnish a variety of character combinations from which to select; there must be inbreeding to isolate the combinations desired." The practical utilization of hybrid vigor is pictured also, a fairly common practice in live stock breeding, a rare one in plants other than maize, for which the authors commend a double crossing system.

The two concluding chapters present applications to the human race. Although avowedly less exact than the earlier chapters, these are in a sense the most interesting of all, as may appear in the following summarizing quotations.

"Owing to the existence of serious recessive traits there is objection to indiscriminate, irrational, intensive inbreeding in man; yet inbreeding is the surest means of establishing families which as a whole are of high value to

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[2] JONES, D. F., Bearing of heterosis on double fertilization. BOT. GAZ. **65**:324–333. *figs.* 3. 1918.

[3] BOT. GAZ. **68**:150. 1919.

[4] BOT. GAZ. **66**:70. 1918.

the community. On the other hand, owing to the complex nature of the mental traits of the highest type, the brightest examples of inherent ability have come and will come from chance mating in the general population, the common people so-called, because of the variability there existent. There can be no permanent aristocracy of brains, because families, no matter how inbred, will remain variable while in existence and will persist but a comparatively short time as close-bred strains. But he is a trifler with little thought of his duty to the state or to himself, who, having ability as a personal endowment, does not scan with care the genealogical record of the family into which he enters." "The hybridization of extremes is undesirable because of the improbability of regaining the merits of the originals, yet hybridization of somewhat nearly related races is almost prerequisite to rapid progress, for from such hybridization comes that moderate amount of variability which presents the possibility of the superindividual, the genius. . . . . Further, there must be periods of more or less inbreeding following racial mixtures, if there is to be any high probability of isolating desirable extremes. A third essential in the production of racial stamina is that the ingredients in the melting pot be sound at the beginning, for one does not improve the amalgam by putting in dross."

One of the most valuable features of the book is the admirable bibliography of 225 titles.—M. C. COULTER.

NOTES FOR STUDENTS

Temperature and the cobalt chloride method of measuring transpiration.—In the improvement by LIVINGSTON and SHREVE[5] of STAHL'S cobalt method of measuring transpiration, one question has remained unanswered, namely, Is it sufficiently accurate to regard the temperature of the slip as it lies on the leaf as being the same as that of the surrounding air? SHREVE[6] has answered this question by making use of a thermo-electrical method for measuring leaf temperatures. This method differs from previous ones in the avoidance of the wounding of the leaf and the resulting temperature complications. Using this method, SHREVE has demonstrated that both in the determination of the index of transpiring power by cobalt slips, and in the standardizing of the slips themselves over a porous evaporating surface, no error results from using the temperature of the air surrounding the apparatus instead of the temperature of the slips themselves.—S. V. EATON.

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[5] LIVINGSTON, B. E., The resistance offered by leaves to transpirational water loss. Plant World **16**:1–35. 1913.

LIVINGSTON, B. E., and SHREVE, E. B., Improvements in the method for determining the transpiring power of plant surfaces by hygrometric paper. Plant World **19**:287–309. 1916.

[6] SHREVE, E. B., A thermo-electrical method for the determination of leaf temperature. Plant World **22**:100–104. *figs. 2.* 1919.

———, The rôle of temperature in the determination of transpiring power of leaves by hygrometric paper. Plant World **22**:172–180. *fig. 1.* 1919.

Anatomy of strand plants.—The eastern shore of Madagascar, characterized by uniformly high temperature, constant winds, and considerable rainfall, has as its principal strand communities two associations characterized respectively by *Ipomea Pes-caprae* and *Barringtonia*. The plants of the former have been examined by DENIS,[7] who finds them, thus exposed to conditions of high transpiration, induced by great insolation and rapid air movement, almost without any special development of epidermal protection, but possessing varying degrees of fleshiness with water-storing tissue rather well developed. One group shows isolateral fleshy structure with the water tissue centrally placed, another possesses bifacial leaves, less fleshiness, and peripheral water tissue. These structural tendencies toward fleshiness are related by the author to the saline character of the beach; the development of water-storing tissue and the early lignification of the roots to the high rate of transpiration; and the abundance of palisade tissue to brilliancy of both the direct and the reflected sunlight. The details of structure are given in the text and in the drawings of leaf sections.—GEO. D. FULLER.

Snow and timber line.—From studies made in the Pyrenees, BOUGET[8] has reached conclusions regarding the influence of snow upon alpine and subalpine vegetation not unlike those of SHAW[9] from a study of the Selkirks more than a decade ago. In the higher altitudes the duration of the snow is related to the local topographic relief, and its persistence during the growing season profoundly influences the character of the vegetation. In depressions it collects during the winter and remaining late in the season gives rise to a rather mesophytic herbaceous community consisting of a mixture of lowland and alpine forms. In contrast, the relative absence of snow upon the ridges and at the same altitude produces a xerophytic vegetation in which trees and woody plants are conspicuous. Thus the upper limit of trees or timber line is much higher upon ridges than along depressions.—GEO. D. FULLER.

Action of enzymes on cellulose.—PRINGSHEIM and MAGNUS-VON MERKATZ[10] point out that dextrines from both starch and glycogen are split to maltose by diastase. They raise the question whether diastase has a similar effect on cellulose dextrine. By using MADSEN'S acetylization method they gained cellulose dextrine from cotton that was soluble in water and

[7] DENIS, MARCEL, Recherches anatomiques sur quelques plantes littorales de Madagascar. Rev. Gén. Botanique **31**:33–52, 115–120, 129–142. *pl. 1. figs. 12.* 1919.

[8] BOUGET, J., De l'influence des neiges sur la répartition des différents végétaux à mène altitude dans les zones élevées des Pyrénées. Rev. Gen. Bot. **30**:305–320. 1918.

[9] SHAW, C. H., The causes of timber line on mountains; the rôle of snow. Plant World **12**:169–181. *figs. 4.* 1909.

[10] PRINGSHEIM, H., and MAGNUS-VON MERKATZ, A., Fermentversuche an Zellulose abbauprodukten. Hoppe-Seyler Zeit. Physiol. Chem. **105**:173–178. 1919.

gave no osazone reaction. The dextrine thus obtained is strongly reducing to Fehling's solution, and is considered by the authors as the end dextrine of cellulose. Diastase will not split cellulose dextrine. They also derived zellobiose by the MADSEN method. The contents of the first stomach of cattle, the intestine, and the pancreas bore no enzyme that would split zellobiose. They conclude that the splitting of this substance in the alimentary canal of the cattle must be due to cellulose bacteria.—WM. CROCKER.

Ecological diversity and generic coefficients.—The principle first enunciated by JACCARD, and noted in this journal,[11] that the ratio between species and genera, or the generic coefficients, varies inversely with the diversity of the habitat conditions, has received additional support from the investigations of DUFRENOY[12] upon the distribution of parasitic fungi in different habitats. Diversity of ecological conditions was found at altitudes of 1100 m. to 2000 m. in the valley of Barèges, where the generic coefficient for rusts was 20 per cent and for all fungi 40 per cent. Contrasted with this were the uniform conditions in a wheat field showing generic coefficients for its fungi of 70 per cent, and upon sand dunes with coefficients ranging from 90 to 100 per cent.—GEO. D. FULLER.

Lignins.—PRINGSHEIM and MAGNUS,[13] in a study of lignins, have obtained some interesting results. When wood or straw is treated with sodium hydrate in the cold, all the acetic acid liberated is derived from the lignins of these materials. When these materials are boiled with sodium hydrate, either under pressure or otherwise, most of the acetic acid formed is derived from the lignins; but a small part is derived from the cellulose and none from the pentoses. The lignin of the white beech yields about 37.85 per cent of its weight of acetic acid, and the lignin of conifer wood about 19.48 per cent. —WM. CROCKER.

Dioecism in Thalictrum.—SCHAFFNER[14] has studied *Thalictrum dasycarpum* in reference to intergrades between the monoecious and dioecious condition. It seems to be a peculiarly favorable form for this purpose, and almost every conceivable intermediate in the expression of "maleness" and "femaleness" was found. The author rightly calls attention to the fact that the physiological and ecological factors concerned in these various expressions must be taken into consideration for an understanding of the evolutionary changes leading from the bisporangiate to the monosporangiate condition.—J. M. C.

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[11] BOT. GAZ. 57:540. 1914.

[12] DUFRENOY, J., Diversité écologique et coefficients génériques. Bull. Trim. Soc. Mycol. Fr. 35:27–46. 1919.

[13] PRINGSHEIM, H., and MAGNUS, H., Über den Acetylgehalt des Lignins. Hoppe-Seyler Zeit. Physiol. Chem. 105:179–186. 1919.

[14] SCHAFFNER, J. H., Dioeciousness in *Thalictrum dasycarpum*. Ohio Jour. Sci. 20:25–34. 1919.

Fungi of North Carolina.—COKER[15] has published a systematic account of certain genera of fungi occurring in North Carolina, illustrated by remarkably fine plates. *Craterellus* is represented by 7 species and *Cantharellus* by 12. *Eomycenella*, *Tragia*, and *Nyctalis* are each represented by a single species. A very complete key to the genera of gill fungi (55 genera) is also included. —J. M. C.

New genus of Pyrenomycetes.—Fitzpatrick[16] has described a new genus (*Rostronitschkia*) of Pyrenomycetes from Porto Rico and Jamaica, parasitic on the leaves of *Gesneria albiflora*. The species has been known for some time, and described by REHM (in litt.) as a new species of *Nitschkia* (*N. nervinicola*). FITZPATRICK has concluded that it is distinct enough from that genus to be entitled to separate generic rank.—J. M. C.

Mutation.—Costantin[17] has published a full discussion of the status of the theory of mutation, weighing the evidence for and against it, as presented in the extensive literature of the subject. His conclusion is that, in spite of the violent assaults against it, "la theorie de la mutation reste debout." The details of the discussion will be well worth consulting by those interested in this controversy.—J. M. C.

Suspensor of Capsella.—SOUÈGES[18] has made a remarkably detailed study of the early embryogeny of *Capsella*, especially in reference to the suspensor. The numerous details cannot be repeated in a brief review, but they should become familar to morphologists. That so much could be obtained from a form so commonly studied is remarkable.—J. M. C.

Tropical American Eupatoriums.—ROBINSON,[19] in continuing his studies on the South American species of *Eupatorium*, has paid particular attention to those of Peru and Bolivia. In the present contribution 37 new species are described, and a review of the Peruvian material recognizes 82 species. —J. M. C.

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[15] COKER, W. C., *Craterellus*, *Cantharellus*, and related genera in North Carolina; with key to the genera of gill fungi. Jour. Elisha Mitchell Sci. Soc. **35**:24–48. *pls. 17*. 1919.

[16] FITZPATRICK, H. M., *Rostronitschkia*, a new genus of Pyrenomycetes. Mycologia **11**:163–167. *pl. 11*. 1919.

[17] COSTANTIN, J., La mutation, état actuel de la question. Ann. Sci. Nat. Botanique X **1**:iii–xxxii. 1919.

[18] SOUÈGES, R., Les premières divisions de l'oeuf et les différenciations du suspenseur chez le *Capsella Bursa-pastoris* Moench. Ann. Sci. Nat. Botanique X **1**:1–28. *figs. 69*. 1919.

[19] ROBINSON, B. L., I. On tropical American Compositae, chiefly Eupatorieae. II. A recension of the Eupatoriums of Peru. Proc. Amer. Acad. **55**:1–88. 1919.

Fumaria and Rupicapnos.—PUGSLEY[20] has published a very detailed revision of *Fumaria* and also of *Rupicapnos* whose species were formerly included in *Fumaria*. In *Fumaria* 46 species are recognized, 6 of which are new; in *Rupicapnos* 20 species are recognized, 7 of which are new.—J. M. C.

New genus of Rubiaceae.—REHDER[21] has described a new genus (*Tetraplasia*) of Rubiaceae from the Liukiu Islands, an evergreen shrub endemic to the islands. It is thought to belong to the Vanguerieae, and is most closely related to *Plectronia* and *Vangueria*.—J. M. C.

New conifers.—WILSON[22] has discussed four new Korean conifers, one, a *Thuja*, having been described in 1919 by NAKAI. The others described by WILSON are a new species and a new form of *Abies*, and a new form of *Larix*. —J. M. C.

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[20] PUGSLEY, H. W., A revision of *Fumaria* and *Rupicapnos*. Jour. Linn. Soc. Bot. 44:233–355. *pls. 9–16.* 1919.

[21] REHDER, ALFRED, *Tetraplasia*, a new genus of Rubiaceae. Jour. Arnold Arboretum 1:190–191. 1920.

[22] WILSON, E. H., Four new conifers from Korea. Jour. Arnold Arboretum 1:186–190. 1920.

GENERAL INDEX

Classified entries will be found under Contributors and Reviewers. New names and names of new genera, species, and varieties are printed in **bold face** type; synonyms in *italic*.

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